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Oyster Production in the Rivers Crouch and Roach, Essex from 1950 to 1954

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I. INTRODUCTION

INVESTIGATION of the conditions necessary for the improvement of oyster stocks in Essex was begun in 1947 by Knight-Jones (1952). In this account, to give continuity, his arrangements of the observations made from 1947 to 1949 is followed.

The improvement in stocks apparent at the end of 1949 continued until heavy losses were caused by the floods of January 1953 (Waugh 1954a). The virtual failures of the spatfalls during 1951, 1952, 1953 and 1954 have prevented further recovery and stocks declined substantially during 1954. Although spatfall during the period under consideration was generally poor, close observation of the production and growth of oyster larvae has led to a clearer understanding of the conditions necessary for success.

Causes of loss of spat have been investigated, including the damage attributable to predation by the oyster drill *Urosalpinx cinerea* (Hancock 1954) and *Asterias rubens* (Hancock 1955). The presence of *Crepidula fornicata* in vast numbers on uncultivated grounds (Mistakidis 1951; Walne 1956) is responsible for losses amongst larval and adult oysters, with which *Crepidula* competes for food and settling space. Flagellates often appear to have been insufficiently abundant to support large oyster populations in competition with other filter feeding organisms.

Information on the growth-rate, abundance and survival of the larvae has been obtained from routine plankton samples to establish relationships with environmental conditions. These observations, made from 1950 to 1954, form the basis of this account.

II. LOCATION OF GROUNDS

The estuaries of the rivers Crouch and Roach have been described previously, by Knight-Jones (1952) who indicated the oyster layings owned or leased by the Ministry of Agriculture, Fisheries and Food. However, in 1953, three additional layings were acquired; one at Holliwell and two in Althorne Creek (Fig. 1). At the same time the lease of the Creeksea ground was allowed to lapse. The Holliwell laying was chosen because it provided a deep water oyster ground in the lower Crouch, reputed to have been good for fattening in former years. The Althorne Creek layings, over which the water normally bears less silt, were acquired in order to study the differences in benthic populations and oyster growth produced by less turbulent conditions.

III. METEOROLOGICAL AND HYDROGRAPHIC OBSERVATIONS

Rainfall in the Burnham area is normally low. Great Wakering, 5 miles south of Burnham, has the lowest rainfall in the United Kingdom (Met. Rep. 1955). The average for the years from 1949 to 1954 was 20·09 inches per annum. Rainfall tends to be slightly greater in summer and autumn than in winter and spring (Table 1). Heavy rain in the latter part of 1950 and throughout 1951 led to poor condition of the oysters and contributed to the failure of the spat in 1951.

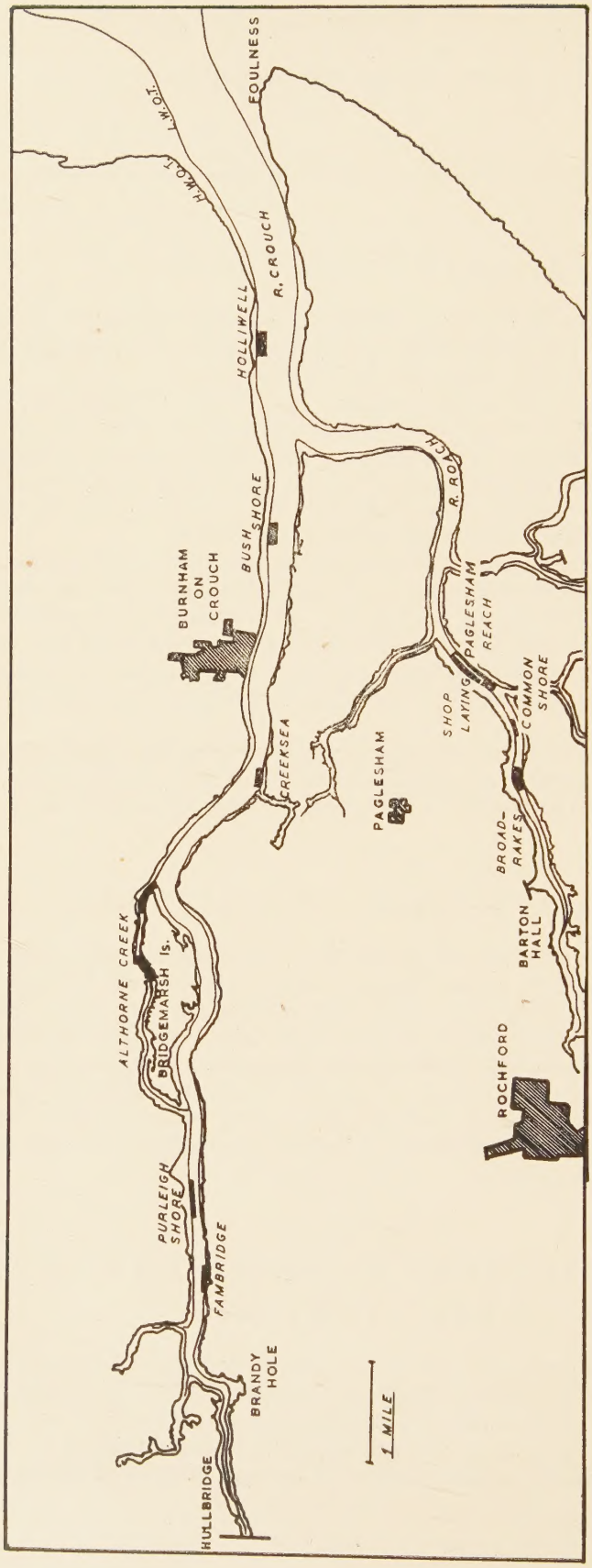

Fig. 1. *Map showing location of oyster grounds, in black, owned or leased by the Ministry in the rivers Crouch and Roach.*

Table 1: Showing annual and seasonal rainfall at Burnham. Records have been split into four three-monthly seasons, starting with December of one year and carrying through to November 30 of the next

Year	1 *Dec.*–28 *Feb.* *in.*	1 *Mar.*–31 *May* *in.*	1 *June*–31 *Aug.* *in.*	1 *Sept.*–30 *Nov.* *in.*	*Total annual rainfall in.*
1948–49	3·03	4·10	1·88	8·54	17·55
1949–50	4·79	3·47	3·78	6·02	18·06
1950–51	6·75	6·15	5·95	6·29	25·14
1951–52	3·03	5·97	4·93	9·05	22·98
1952–53	3·00	2·77	6·82	4·63	17·22
1953–54	3·35	3·66	7·48	5·10	19·59
Average	3·99	4·35	5·14	6·61	20·09

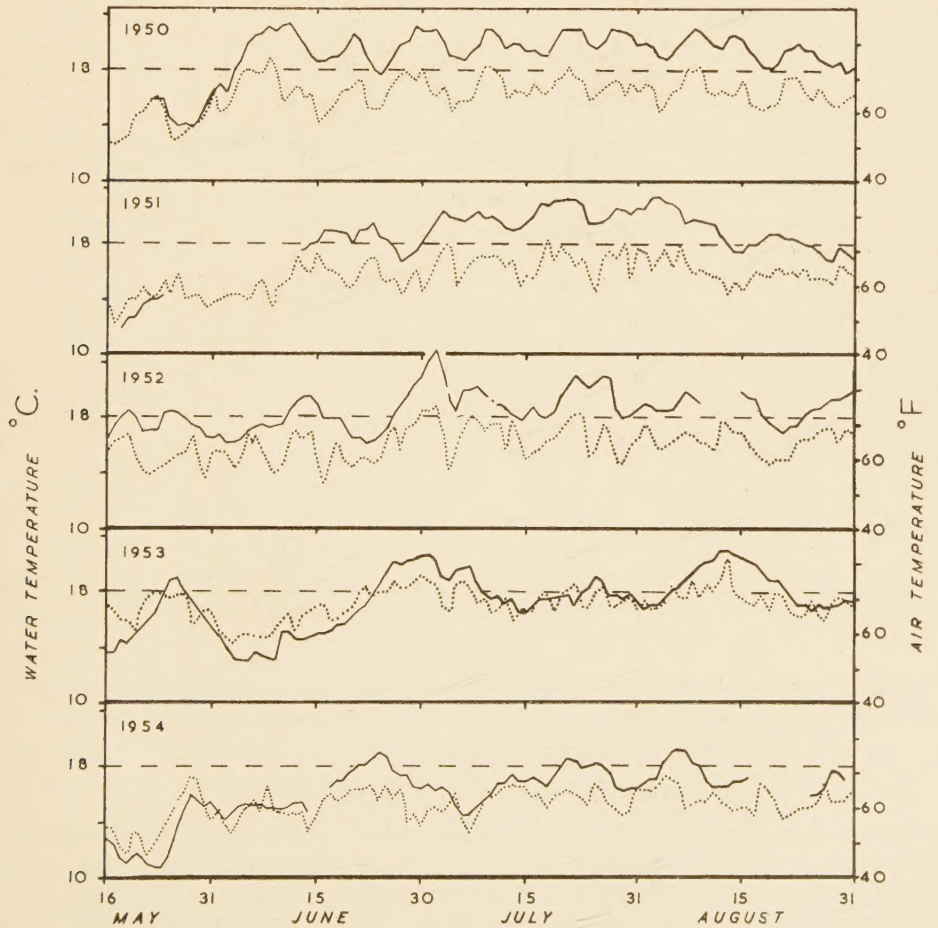

Fig. 2. *Showing the mean daily water temperature in °C (continuous line) in river Roach and the mean daily air temperature in °F (dotted line) at Burnham, during the five years.*

Summer air temperatures are, in general, high for Britain and have a marked effect on water temperature. Extensive sand banks outside, and muddy shores inside, the rivers warm up quickly in the sun. They give up their heat to the water when flooded, so that temperature fluctuations of as much as 4°C. between ebb and flood tides often occur. The net effect, however, is that changing air temperature is closely followed by changing water temperature (Fig. 2). As air temperatures in Britain fluctuate widely it is, therefore, not unusual for water temperatures suitable for breeding to be reached early in the season and be succeeded by temperatures unsuitable for rapid growth and good survival of oyster larvae. It was only in 1950 that relatively stable air and water temperatures were experienced; in that year there was the best spatfall for several seasons, although as we shall see, it was claimed only as moderate.

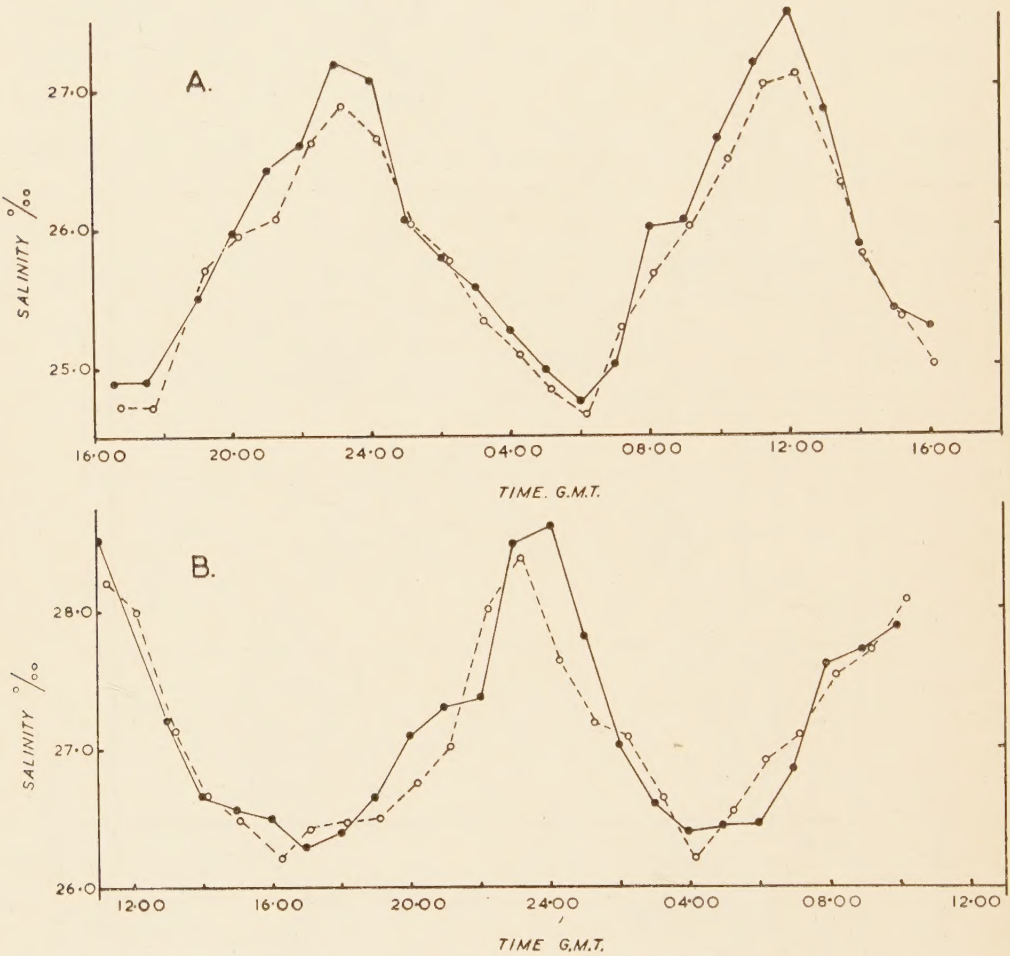

Fig. 3. *Salinity observations at Fambridge during the tidal cycle. Surface salinities are indicated by open circles and salinities from* 1 *M. above the bottom by solid circles.*

A. Observations made from May 3 *to* 4, 1951.

B. Observations made from May 19 *to* 20, 1951.

For most of the year, water approaching full salinity extends up river to near the limits of oyster production—Hullbridge in the river Crouch and Barton Hall Creek in the river Roach. Normal rainfall has little effect on salinity, as the catchment area is small, and drainage from the land negligible, in proportion to the volume of tidal water. After prolonged wet weather, when the low-lying land becomes water-logged, there is a direct run off and salinity in the upper reaches may remain low for several weeks. This occurred, for example, in the winter of 1950-51, when the salinity at low water at Fambridge dropped as low as

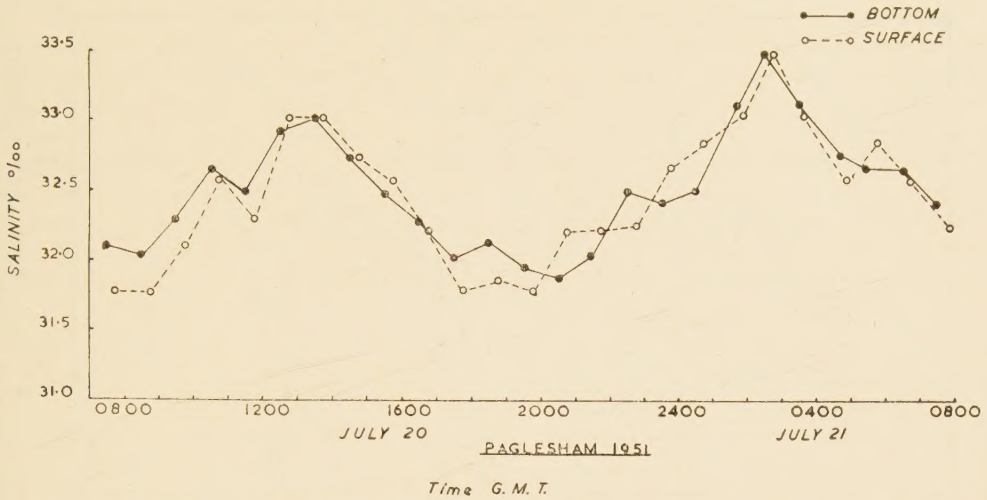

Fig. 4. *Surface and bottom salinities as recorded in Paglesham Reach on July* 20 *and* 21, 1951. *Otherwise as for Fig.* 3.

11·0‰ and remained at or below 20·0‰, at low water, from early February until mid March. In normal years, if the salinity at low water in this area drops below 20·0‰ at all, it remains low only for a few days. Extreme cold combined with low salinity is the principal cause of heavy winter losses (see Section XI).

It was assumed that turbulence would prevent layering of the river water but, to obtain information on this point, a series of surface and bottom salinity samples were taken at different times at Fambridge and Paglesham. In May 1951, when the two Fambridge samples were taken, the salinities were still low—of the order of 25·0‰ (Fig. 3)—but in July, at Paglesham, they were more normal, the lowest being 31·75‰ (Fig. 4). There was no evidence of a halicline but, on the other hand, there was in all three cases a disruption of the curves of salinity during the flood tide. The apparent anomaly has since been shown to be due to fluctuations in rates of water movement. Measurements of flow, using submarine current indicators (for description see Carruthers, 1955), showed that the changing velocity of the tide did not conform to a single sine curve, but that, on the flood, there was a reduction in velocity at half tide and, on the ebb, there was a sudden surge, maximum velocity being reached at about one and a half hours after high slack water. This effect, apparent at Fambridge, Paglesham and at Ness Hole near the mouth of the Crouch (Fig. 5), is characteristic of a shallow water tide and in this instance is $^1/_6$ diurnal in nature (Doodson & Warburg 1941). Such a phenomenon explains the disruption of the salinity curves mentioned earlier. It is thus confirmed that there is no layering.

Wind direction and speed (Figs. 5b & 5c) influence current velocity in the upper layers and may affect the amount of exchange of water between river and sea. For example, strong westerly winds may be associated with substantial losses of river water and of larvae, out to sea. Further studies of wind influence are being made.

pH occasionally fell as low as 7·7 in the winter months and 7·8 in the summer. Generally, however, it remained between 7·9 and 8·1 during the breeding season. Fluctuations in pH were not always clearly related to changing phytoplankton (Fig. 6) but the comparatively low pH values may be due to the relative scarcity of fixed algae and comparatively small numbers of phytoplankton organisms in the water.

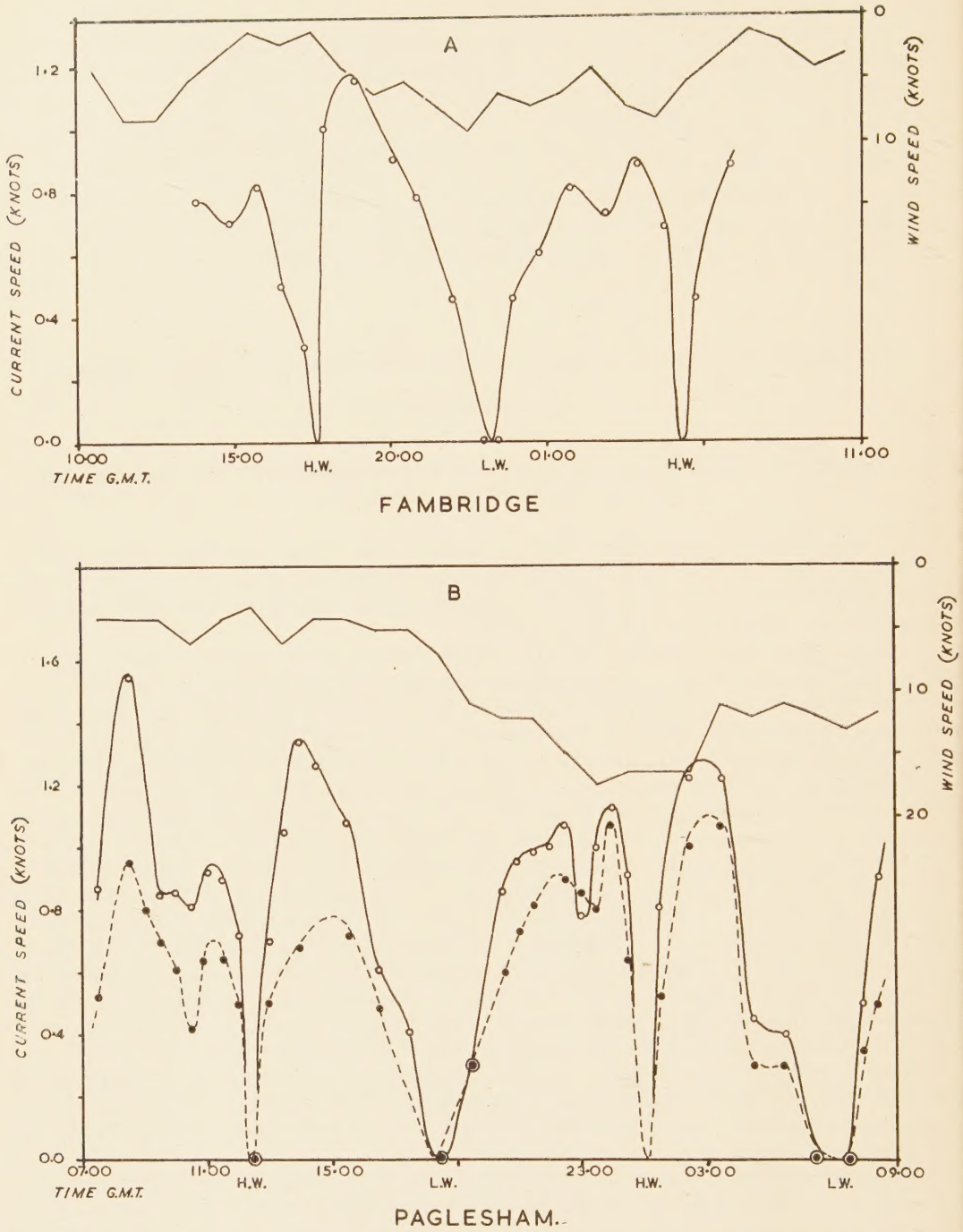

Fig. 5A and 5B. *Graphs showing current velocity and wind speed (inverted scale) at A Fambridge on August* 4 *and* 5, 1954 *and B Paglesham on September* 28, 1954.

Current velocity was measured at a height of 4 M. (open circles) and 1 M. (solid circles) above the bottom. Wind velocity increased considerably at Paglesham during the second floor tide and the direction varied between 200° and 260°. As the bearing of Paglesham Reach is appoximately 220°, this meant that the wind was blowing virtually straight down stream against the tide.

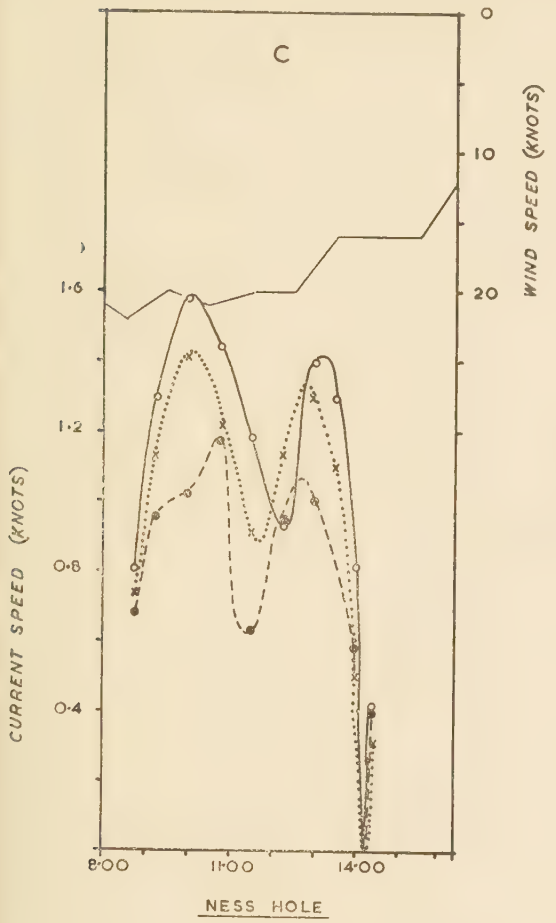

Fig. 5C. *Showing current velocity* 8 *M.* (*open circles*), 4 *M.* (*crosses*) *and* 1 *M.* (*solid circles*) *above the bottom during the flood tide of September* 30, 1954 *at Ness Hole in the lower Crouch. Throughout the period the wind blew from between* 230° *and* 250°, *i.e. against the flood tide.*

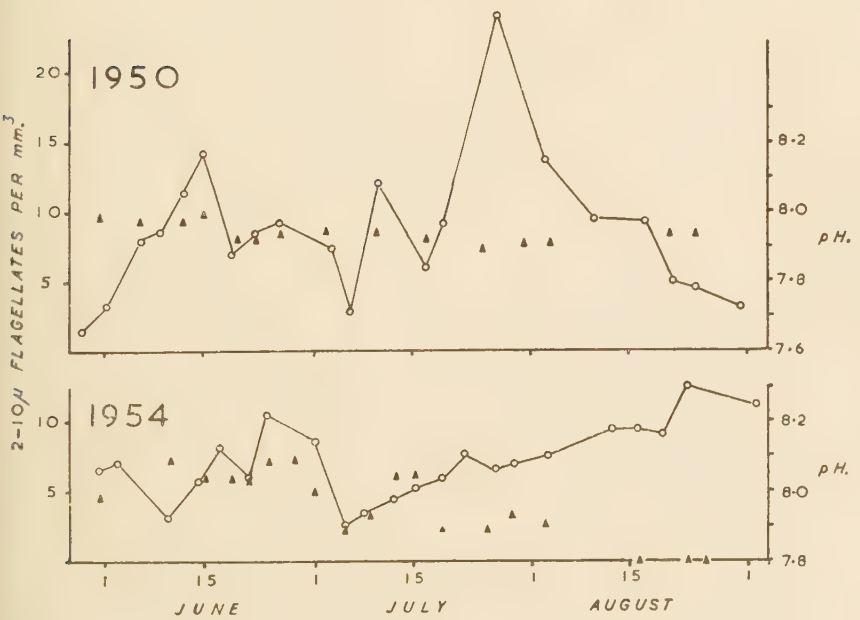

Fig. 6. *Showing the population of* 2-10μ *flagellates per mm*^{3}. (*open circles*) *and the hydrogen ion concentration* (*solid triangles*) *in the river Roach during* 1950 *and* 1954.

IV. NANOPLANKTON

Estimations of the abundance of nanoplankton were made by the method of Cole & Knight-Jones (1949). In view of the importance of flagellates as food of larval organisms (Cole 1936; 1939; Bruce *et al.* 1940), and their rapid multiplication, frequent sampling was required to give an accurate picture. Samples were accordingly collected from two stations in each river twice per week—a total of 8 observations per week. The samples were taken at low water in the same place and at the same time as the plankton samples. Storage in thermos flasks (Waugh 1952) allowed samples to be examined as much as 9 hours after collection. All the samples were collected from just below the surface, as it was thought that there was sufficient turbulence to produce a uniform vertical distribution of the flagellate population.

This frequent sampling revealed rapid fluctuations in the population due to changes in temperature, sunlight, etc. though the limiting factors are still imperfectly understood. In Essex, turbulence, while producing uniform distribution of phytoplankton, also causes great turbidity and exclusion of light at comparatively shallow depths. The scarcity of sublittoral algae, where there is a sufficiently firm substrate, suggests inability to survive through lack of light; flagellates are probably similarly affected. 10 cm. columns of water from Bush Shore absorbed between 60 and 94% of light of wavelength 600°A. The degree of absorption varied with the state of wind and tide. Thus wind influence on survival of food organisms and larvae is important.

The use of the 4 mm. objective while counting precluded the certain identification of most of the nanoplankton algae encountered and it had to be assumed that the population contained a sufficient number of utilisable forms, though there are some (Loosanoff 1954; Walne 1956) that are unsuitable as food for oyster larvae.

During 1950 a high density of flagellates was present throughout most of the season with peaks at the time of liberation of the oyster larvae (Waugh 1952). There was a positive correlation between growth, spatfall and flagellate abundance. In 1951, when flagellate production was at its lowest at the time of liberation, there was no growth of larvae. In 1952, 1953 and 1954 numbers were lower than in 1950, but greater than in 1951, and there were limited spatfalls (Waugh 1953; 1954b; 1956). It seems reasonable to conclude that abundance of flagellates is a major factor directly influencing larval growth.

Grazing by larvae and by other filter feeders is not easy to illustrate but in 1950 the peak populations of flagellates were recorded a day or two before the maximum numbers of larvae were found; a drop in the flagellate population occurred at the time of maximum feeding. In 1951 the low numbers of flagellates associated with the peak larval population may have resulted from grazing. Certainly when larvae occur at the rate of 1,500 or more per 100 litres, they constitute, or appear to constitute, a major part of the filter feeding plankton. The qualification is made as the more active zooplankton organisms are not collected by pump sampling but swim away from the intake. For example, barnacle nauplii were not normally very abundant in the samples, and the cyprid larvae were even less so, despite the immense numbers settling.

Though other larval organisms, particularly gastropod veligers, were frequent in the samples, it was noticeable, particularly in 1951, that their numbers were much reduced at times when spatfall was poor. In 1951, when there was no oyster spatfall, the settlement of *Elminius modestus* (see Section XI) and *Crepidula fornicata* was also much reduced. Temperature, as the common factor influencing growth and survival of all these filter feeding forms, could be discounted, as the critical level for *Crepidula* and *Elminius* (Werner 1948; Chipperfield 1951; Crisp & Davies 1955) is several degrees lower than for *Ostrea* (Orton 1936). Salinity, whilst lower than normal, was still relatively high, but the flagellate counts were down. This was the only factor which seemed likely to exert a common influence on all types of filter feeding organisms.

The abundance of other phytoplanktonic organisms tended to vary with that of the flagellates, thus fat oysters could be expected in a year of good spatfall. This was true in 1950 but the converse applied in 1951. Condition in 1952 and 1953 was moderate and in 1954 was good. In the last-named year, though flagellates were moderately abundant,

water temperatures were so low as apparently to inhibit some spawning, with the result that the oysters retained more nutrient material than normal at the end of the season and passed into the resting stage in better condition than after warmer summers.

Dr. Butcher tells me that his surveys made during 1953 and 1954 indicate that the greatest densities of nanoplankton organisms occur in the pools high up on the saltings and in brackish ditches behind the sea walls. High spring tides, covering the saltings, wash out these pools and so augment the flagellate population of the river system, though probably only for a short time. So many factors appear to influence the multiplication and survival

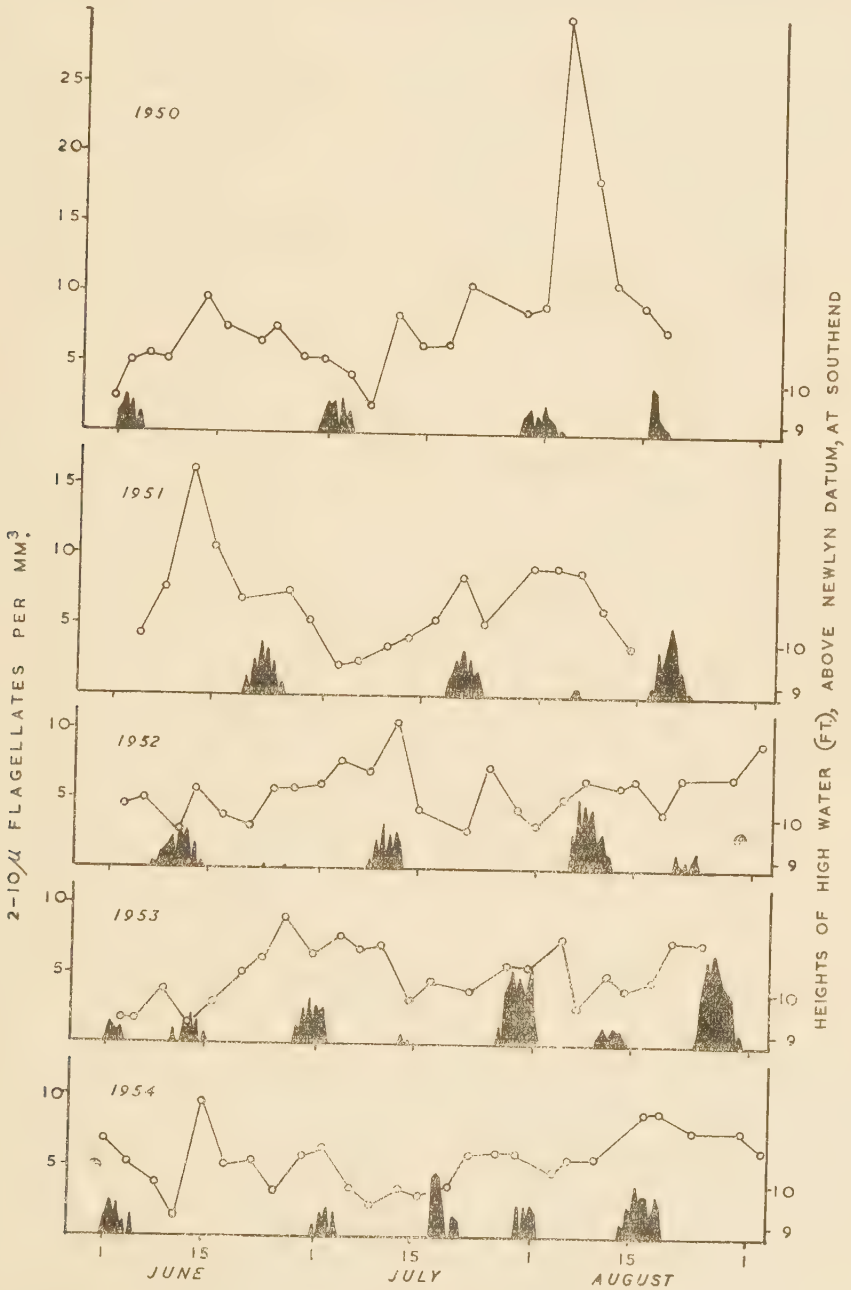

Fig. 7. *Abundance of* 2-10μ *flagellates in the river Crouch in relation to tides which covered the saltings. All tides which were more than* 8′ 9″ *above Newlyn Datum, as recorded at Southend, are considered to have flooded the saltings.*

of flagellates that it is difficult to distinguish this one effect of tide from the others. No tide gauge records were available for the river Crouch but records of tidal heights as recorded at Southend were kindly made available by the Port of London Authority. From these records, and occasional observations of tides which covered the saltings at Burnham, it was possible to judge at what height, as recorded at Southend, the tide would flood the saltings in the Crouch-Roach system. Often the first of the saltings tides resulted in a fall in the flagellate population. This suggests that the clay which was washed off the shores and produced extremely turbid water, at the time of spring tides, resulted in reduced light penetration and a slower rate of division of the flagellates (Verduin 1954). At neap tides, on the other hand, when the water was calmer and light penetration greater, multiplication of flagellates seemed to be better (Fig. 7). Enrichment of the upper Crouch with superphosphate in 1954 resulted in only a slight increase in the flagellate population. It was found that the natural phosphorus content of the water was high and that it was increased at spring tides and during turbulent conditions brought about by strong winds. This effect was probably due to release of phosphate from the stirred-up mud (Stephenson 1949). It was also found that the effects of enrichment were quite long lasting—the enriched water being held in the upper reaches of the river. Detailed results of these experiments will be published later. On the whole the conditions in the main body of water seem more important than additions of flagellates from high water pools.

V. SAMPLING OYSTER LARVAE

The method of sampling was that used by Knight-Jones (1952). 100 l. samples, taken from a depth of 2 m. by centrifugal pump, were collected from three widely spaced stations in each river at approximately 3 day intervals (Fig. 8). The samples were taken at low water at all 6 stations. During most seasons spatfall and larval growth and abundance showed good agreement but their distribution varied, apparently due to the liberation of the larvae at slightly different times in relation to the tidal cycle. The importance of this is discussed in Section VII.

At the end of the 1953 season and in 1954 an additional sampling station (Branklet, Fig. 8) was used in the river Crouch, slightly upstream from the mouth of the river Roach. Samples taken there would show any down-river dispersion of larvae below Burnham, but would be unaffected by any larvae draining out from the Roach. These latter larvae, even if carried up the Crouch on the flood tide, would normally occur at this point on the subsequent low water only if there was no residual tidal movement down river. These samples were, therefore, considered to contain predominantly Crouch larvae, though strong easterly winds might occasionally have driven Roach larvae further into the Crouch.

VI. SPAWNING PERIODICITY

Spawning in relation to tidal periodicity has been discussed by Orton (1926), Korringa (1941; 1947 and 1952) and Knight-Jones (1952). The last-named also refers to the periodicity observable in the results of Herman (1938) and Ladouce (1938). During the five years here discussed, spawning occurred at spring tides in only a slight majority of cases though it did occur more frequently when the tides were increasing to springs rather than decreasing to neaps (Figs. 9-10). The first mass spawning of the season was more often associated with a rise in temperature above 16°C. than with a particular state of the tide. Tides, though they may influence the onset of spawning, appear to be of minor importance. Obviously the degree of maturation of the gonads at the beginning of the season is most important and would be influenced by the preceding temperatures. Orton (1936) admits the probability of time and temperature influencing development. Spärck (1925) and Nelson (1928) also stress the importance of the early temperatures in affecting maturation; certainly adverse

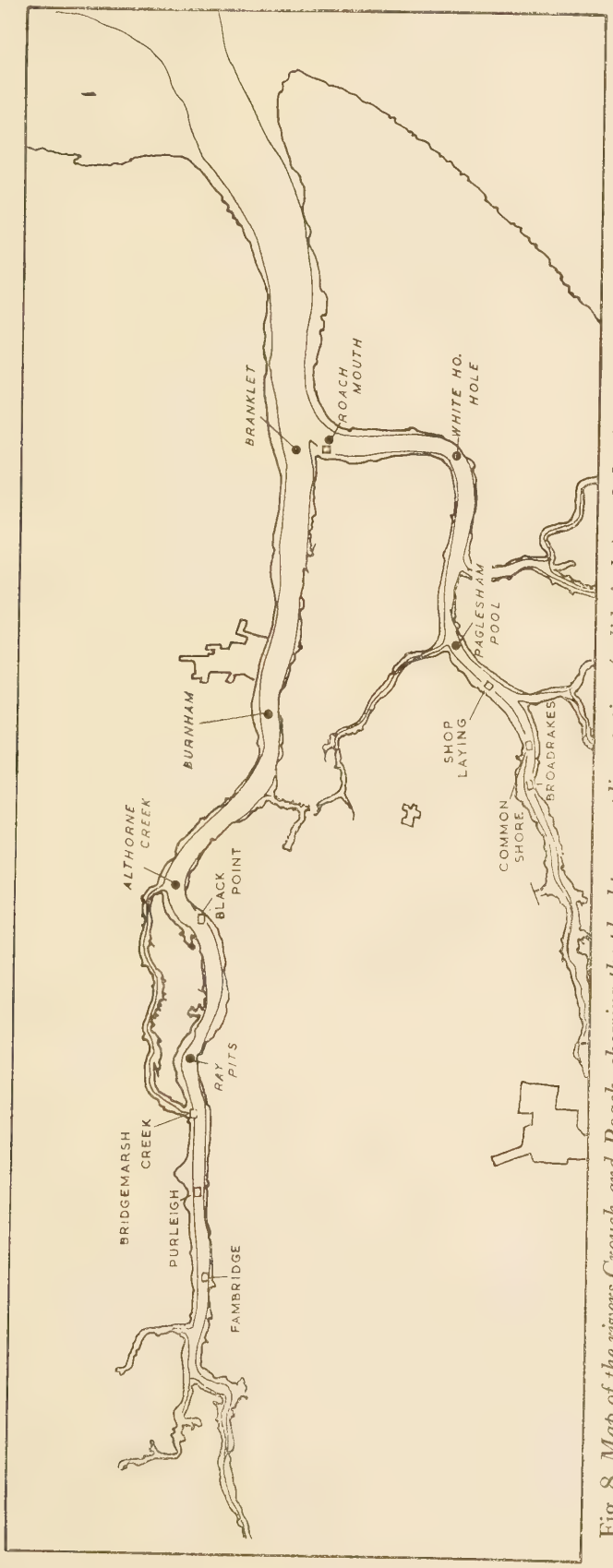

Fig. 8. *Map of the rivers Crouch and Roach, showing the plankton sampling stations (solid circles) and the sites of frameworks of artificial collectors (open squares) referred to in the text.*

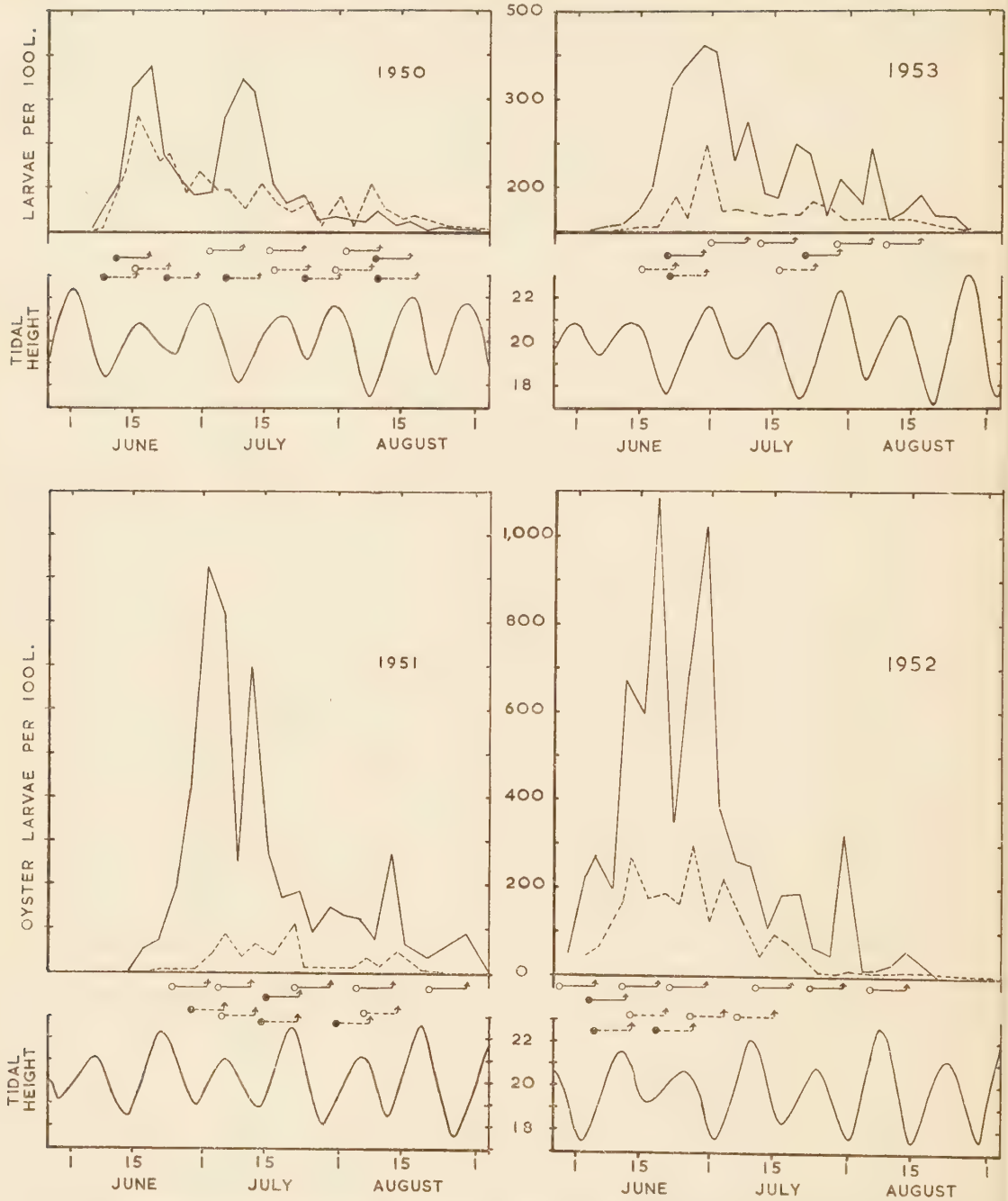

Fig. 9. *Spawning in relation to tidal periodicity* 1950 *to* 1953. *Numbers of larvae per* 100 *litres in the river Crouch (broken line) and river Roach (continuous line) are shown together with the mean predicted levels of high water at London Bridge. Arrows pointing to the liberations have been produced backwards assuming an incubatory period of* 8 *days, to indicate expected time of spawning. An open circle indicates when this coincides with spring tides and a solid circle when it coincides with neaps.*

conditions can delay the onset of spawning and liberation, as in 1951. In 1950 there was no evidence of abnormal water temperatures in April and May, yet liberation and, presumably, spawning was delayed for some time after the water exceeded 16°C. and was also apparently uninfluenced by the state of the tide.

It has been assumed that, provided water temperatures are satisfactory, normal growth and development of the reproductive organs will follow, though in fact these must also be dependent upon the abundance of food organisms and detritus (Loosanoff & Engle 1942; Loosanoff & Tommers 1948).

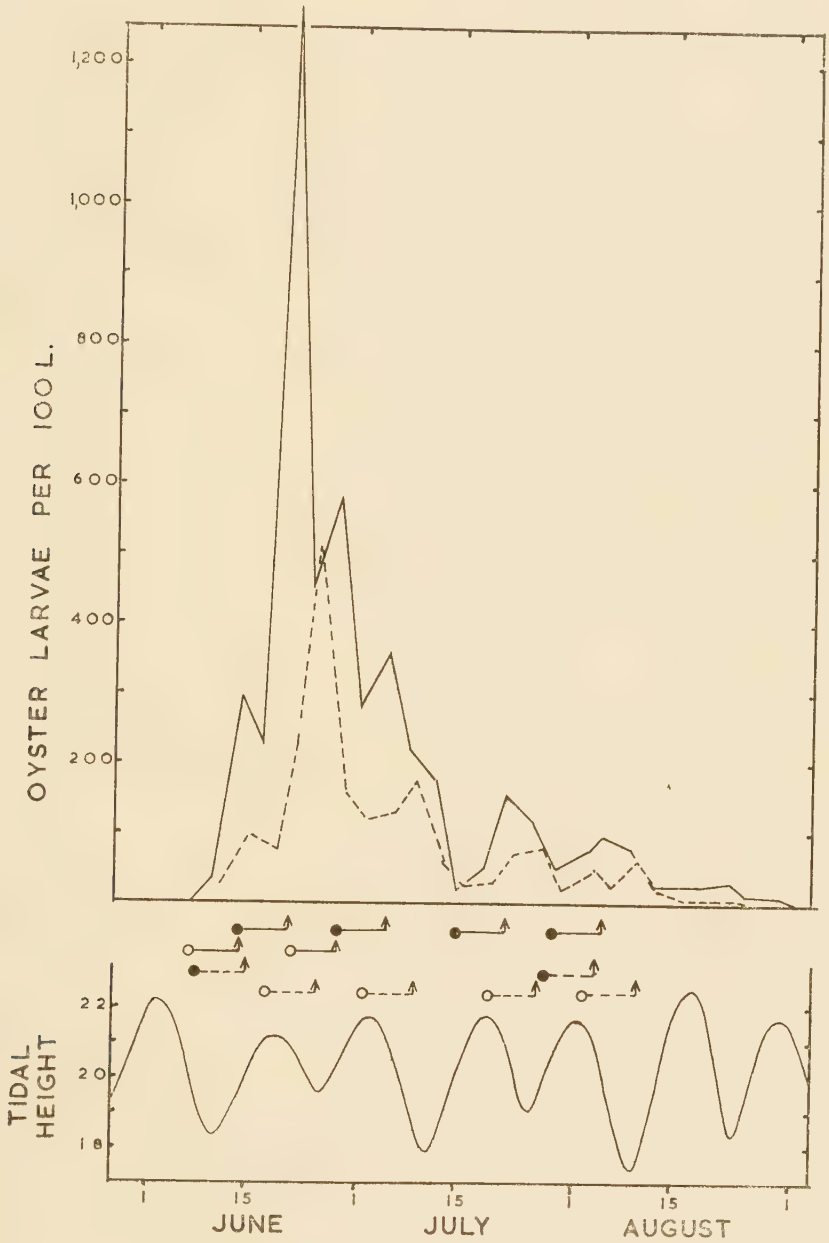

Fig. 10. *Spawning in relation to tidal periodicity* 1954, *otherwise as for Fig.* 9.

VII. LIBERATION DURING THE TIDAL CYCLE

Knight-Jones (1952) showed that whilst liberations took place in all weathers, and at varying salinities, they did not occur with uniform frequency throughout the tidal cycle. He concluded that liberations of larvae occurred at or about high water and this was supported by the distribution of larvae in the river Roach. There the main stocks of oysters were in the

Paglesham area and apart from a small concentration at Whitehouse Hole (Fig. 8) there were none towards the river's mouth. The fact that the greatest numbers of larvae appeared at the mouth at low water, and the fewest over the stocks at Paglesham, led him to conclude that the larvae must have been liberated at or about high water and swept down river on the subsequent ebb. Results obtained to date support this contention with few exceptions. Knight-Jones only described the movements of larvae in the river Roach because, in that river, the distribution of the stocks of oysters enabled him to 'pin-point' the breeding locality. However, the distribution of larvae in the river Crouch followed a somewhat similar pattern in 1948 and 1949, in that there were more larvae at the downstream station at low water than at those up-river; this also held good from 1951 to 1954.

In 1950 the pattern was reversed in the Crouch and slightly different in the river Roach. Stocks of oysters in the river Crouch were fairly widely distributed and not particularly heavy. There were few live oysters in the upper reaches, above Bridgemarsh Island, following the severe winter of 1946/47, except for approximately 10,000 laid in Brandey Hole (Fig. 1), in May, 1947, by a local Company. The 1947 spatfall was believed to be meagre; those of 1948 and 1949 were reasonably good, though the main settlement was in the lower reaches of the river. It seemed unlikely, therefore, that there were many oysters more than two years old in the upper Crouch by the summer of 1950, yet in that season the numbers of larvae in the water there were almost as great as in the Roach (Waugh 1952). This was the only record of such an occurrence during 8 years' observations. There were far more larvae in the up-river sampling stations than down-river, implying that the Crouch oysters in that season liberated their larvae at low, instead of high water. Yet this alone would not account for the distribution, as the biggest numbers of larvae were collected at the station Ray Pits (Fig. 8) at about the upper limit of oyster survival in 1947. As a result there was, in 1950, a rather dense spatfall in the upper Crouch. Shelbourne (in press) showed in 1951, that, of the population of 18½ m. oysters in the Crouch, 15 m. were 1-year-old, i.e. derived from the 1950 spat.

In the river Roach in 1950 the difference was less apparent. In the upper part of the river, i.e., at Paglesham over the oyster stocks, larvae were almost invariably fewer at low water than at points further downstream. Early in the season, at the time of the first liberation, the greatest number of larvae per 100 litre appeared at Roach Mouth but later they were proportionately more abundant at White House Hole, ca. 1¾ miles upstream. On the basis of a purely piston-like movement this could be explained by the probability that those larvae reaching Roach Mouth just before low water tended to get swept away and, on the subsequent flood, as has been demonstrated by float experiments, were carried up the Crouch. This slight mixing and dispersion at the lower end of the Roach reduced larval numbers, leaving a higher density in the middle reaches.

The relative distribution varied from year to year and can be related to wind and rainfall. In Figs. 11 and 12 the ratios of the relative densities of larvae at Whitehouse Hole and Paglesham have been plotted about those at Roach Mouth—taken as 1. Surface wind speeds and directions were kindly supplied by the Meteorological Office and, from these, 6 hourly means were calculated. The mean bearing of the river Roach was considered to be 70°E of N and where winds were blowing at an angle to this, the appropriate component of their velocity along the direction of the river was calculated using the cosine formula. These winds have been plotted as being either easterly or westerly, i.e., blowing up or down stream respectively. Tidal heights at Southend are also shown.

Throughout the greater part of 1950 the highest density of larvae occurred in the middle reaches of the Roach and the ratios of larval numbers at Whitehouse Hole to those at Roach Mouth were always greatest at neap tides, i.e., when there was least dispersion. In 1951 the highest density occurred at the mouth of the Roach in the majority of cases though one exceptional larval liberation occurred at low tide at Paglesham on July 20 (Fig. 11b). It appeared that there were heavy losses of larvae from the Roach into the Crouch. A probable cause of this was a residual flow down river due to the much heavier rainfall that season. There was no spatfall but there is evidence that the failure was due to other causes (Section VIII).

Larval densities were more often highest in the middle reaches of the river Roach in 1952 (Fig. 11c), but in 1953 there were usually greater numbers at the mouth of the river.

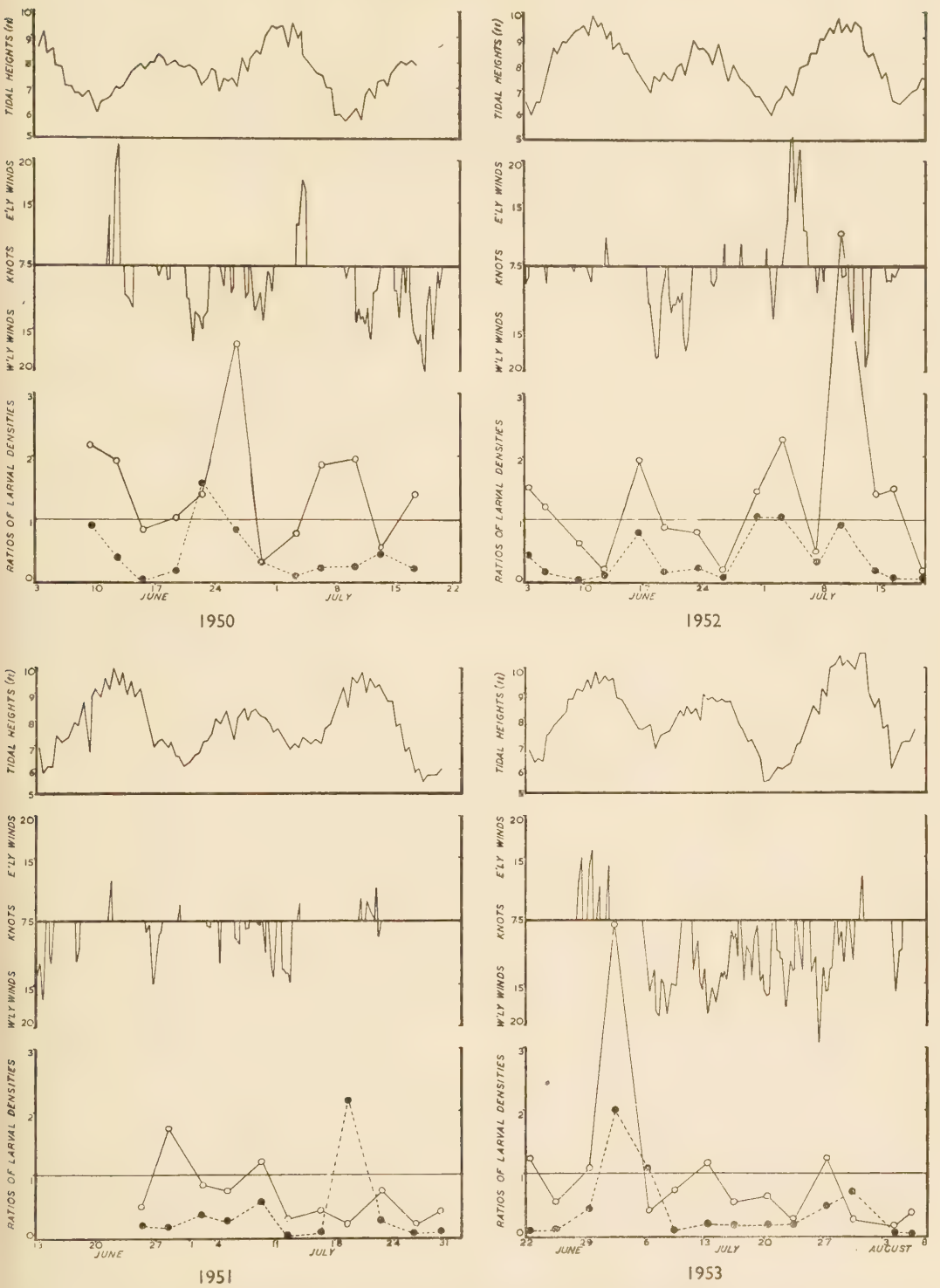

Fig. 11. *Records from* 1950-53 *of heights of high water above Newlyn Datum, as recorded at Southend. Wind velocity or its components blowing East or West, i.e. up or down river and the ratios of the larval densities in the river Roach. The numbers of larvae per unit volume at Roach Mouth are taken as* 1. *Those for White House Hole are indicated by open circles and for Paglesham Reach by solid circles.*

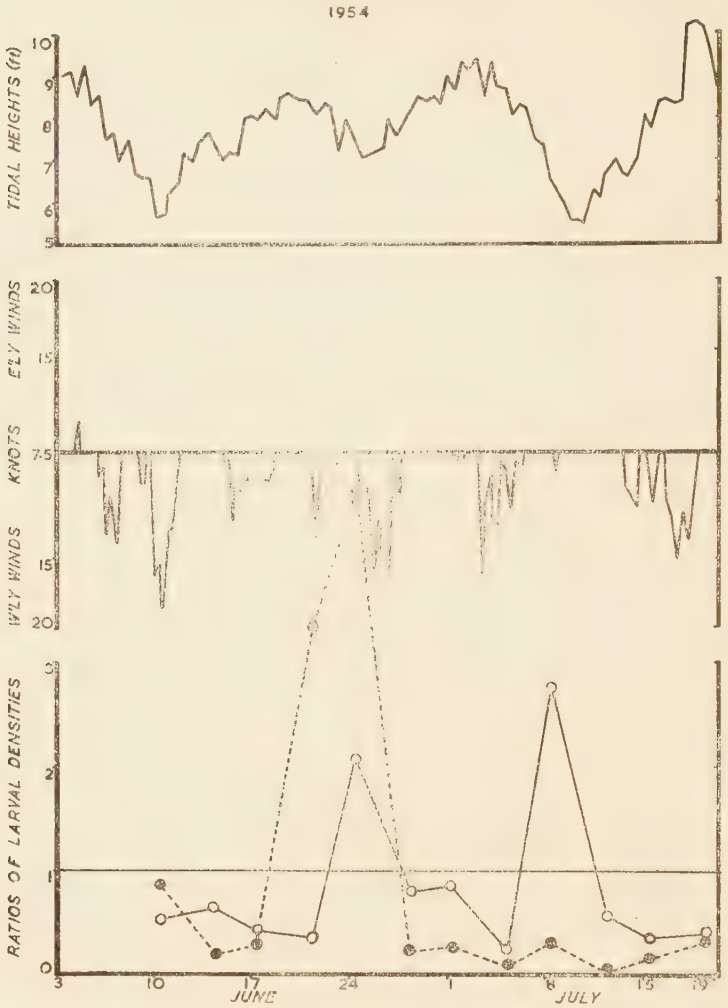

Fig. 12. *Tidal heights, wind velocities and larval densities in the river Roach in* 1954, *otherwise as for Fig.* 11.

In this season the rainfall was normal but there were prolonged westerly winds (Fig. 11d) which probably resulted in dispersal of water and larvae out of the Roach.

In 1954 liberations occurred at low tide in Paglesham Reach but, despite this, larval densities were usually greatest at the mouth of the river Roach. The slow larval development would have led to greater dispersion, and west south west winds, though not as strong as in 1953, again probably contributed to the loss (Fig. 12).

Our observations demonstrate that liberations of larvae must occur almost simultaneously and occupy a comparatively short time. Erdmann (1934) describing the act of liberation, has stated that it may be completed in a few hours though Walne (1956) records extension over 24 hours. However, had the liberations occupied more than about two hours, the distribution of the larvae in the river Roach would have been more uniform than was apparent from the plankton counts.

VIII. GROWTH AND SURVIVAL

Those larvae liberated earliest in the season were usually approximately 0·19 to 0·20 mm. while later in the season, smaller larvae, 0·16 - 0·18 mm. occurred with much greater frequency (Tables 2, 3, 4, 5, 6 and 7). This phenomenon was noted by Korringa (1941) and

Table 2: Numbers of oyster larvae per 100 litre plankton sample in the middle reaches of the river Roach (Whitehouse Hole) at low water, 1950. Small figures indicate numbers of eyed larvae in each size group.

Date	Total larvae	Size distribution (mm.)															Eyed larvae
		0·16	0·17	0·18	0·19	0·20	0·21	0·22	0·23	0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1950																		
June 1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6	6	1	–	–	1	4	–	–	–	–	–	–	–	–	–	–	–	–
9	218	–	–	4	4	29	46	75	38	21	–	1	–	–	–	–	–	–
12	315	–	–	6	17	50	76	64	49	21	13	13^{1}	3^{1}	3^{1}	–	–	–	3
15	777	–	–	16	28	126	201	152	75	63	53	13	14^{2}	25^{19}	6^{6}	5^{5}	–	32
19	1016	–	9	10	78	127	197	186	168	88	49	32^{1}	39^{4}	20^{18}	10^{10}	3^{3}	–	36
22	321	–	-	4	56	72	56	40	16	16	28	9^{1}	15^{2}	6^{6}	2^{2}	1^{1}	–	12
26	303	–	35	57	62	43	30	19	8	11	5	11^{5}	11^{6}	8^{6}	1^{1}	2^{2}	–	20
29	82	–	1	13	13	18	16	6	2	2	5^{4}	4^{4}	2^{2}	-	-	-	-	10
July 3	165	1	4	19	25	34	28	18	5	7	9^{5}	5^{5}	4^{4}	6^{6}	[illegible]	.	.	20
6	595	4	18	65	131	135	91	69	31	21^{3}	14^{1}	11^{2}	4	–	1^{1}	–	–	7
10	739	14	67	153	162	135	112	58	18	9	7^{3}	4^{4}	–	–	–	–	–	7
13	369	6	15	55	55	104	51	22	28	20	4^{4}	1^{1}	5^{5}	1^{1}	2^{2}	–	–	14
17	237	–	–	17	27	79	52	15	12	7	16^{11}	8^{8}	4^{4}	–	–	–	–	23
20	179	1	7	17	31	49	30	15	4	4	4	3^{2}	5^{5}	7^{7}	2^{2}	–	–	16
24	111	2	9	17	32	30	8	4	6	2	1^{1}	–	–	–	–	–	–	1
27	8	–	–	2	2	2	2	–	–	–	–	–	–	–	–	–	–	–
31	28	3	2	5	7	5	1	1	2	2	–	–	–	–	–	–	–	–
Aug. 3	31	1	3	8	10	4	3	1	–	1	–	–	–	–	–	–	–	–
10	122	4	13	32	29	22	8	4	5	3	1^{1}	–	1^{1}	–	–	–	–	2
14	26	–	1	2	7	6	4	3	2	1	–	–	–	–	–	–	–	–
17	29	3	2	4	6	7	3	–	–	1	3	–	–	–	–	–	–	–
21	5	–	–	1	–	2	1	1	–	–	–	–	–	–	–	–	–	–
24	9	–	1	1	2	3	2	–	–	–	–	–	–	–	–	–	–	–
28	7	1	–	–	3	2	–	1	–	–	–	–	–	–	–	–	–	–
31	2	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Sept. 7	7	–	1	–	3	2	1	–	–	–	–	–	–	–	–	–	–	–
11	4	–	–	–	–	2	–	1	1	–	–	–	–	–	–	–	–	–

Table 3: Numbers of oyster larvae per 100 litre plankton sample collected at Burnham at low water in 1950. Small figures indicate eyed larvae in each size group.

Date	*Total larvae*	*Size distribution (mm.)*																*Eyed larvae*
		0·16	0·17	0·18	0·19	0·20	0·21	0·22	0·23	0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1950																		
June 5	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	3	–	–	–	–	1	1	–	–	1	–	–	–	–	–	–	–	–
13	75	–	–	2	4	11	12	6	15	13	7	4	–	1^{1}	–	–	–	1
16	201	–	2	9	20	55	34	27	20	12	14	4	3^{1}	1^{1}	–	–	–	2
21	162	–	–	3	12	35	29	18	26	12	12	3	4^{1}	6^{6}	2^{2}	–	–	9
23	283	–	–	16	24	62	48	27	34	14	24	6	11^{7}	13^{11}	2^{2}	2^{2}	–	22
27	111	–	23	29	20	14	5	8	1	3	1	5^{5}	1^{1}	–	1^{1}	–	–	7
30	112	5	12	14	30	12	14	2	5	5	4^{4}	4^{4}	5^{5}	–	–	–	–	13
July 4	80	2	6	19	13	13	13	6	2	2	2^{2}	1^{1}	–	–	1^{1}	–	–	4
7	162	–	7	43	33	30	23	13	6	3	1^{1}	2^{2}	1^{1}	–	–	–	–	4
11	70	2	2	7	12	16	8	7	4	4	5^{5}	3^{3}	–	–	–	–	–	8
14	249	–	–	12	30	46	47	32	20	19	11^{4}	17^{10}	9^{9}	5^{5}	–	1^{1}	–	29
18	66	–	1	5	10	14	7	4	9	4	5^{3}	3^{3}	1^{1}	–	–	–	–	7
21	48	–	3	5	12	10	10	3	2	3	–	–	–	–	–	–	–	–
25	54	–	–	3	14	19	6	6	3	2	–	1	2^{2}	2^{2}	–	–	–	4
28	18	–	2	2	1	2	2	3	3	2	–	1^{1}	–	–	–	–	–	1
Aug. 1	103	2	17	18	25	13	10	2	5	5	2	1^{1}	1^{1}	–	–	–	–	2
4	28	–	2	10	9	3	2	2	–	–	–	–	–	–	–	–	–	–
8	75	3	8	21	19	15	3	1	1	2	2^{2}	–	–	–	–	–	–	2
11	133	2	3	9	21	20	25	17	17	8	5^{2}	3^{3}	2^{2}	1^{1}	–	–	–	8
15	34	–	–	3	4	7	5	6	2	4	2^{2}	1^{1}	–	–	–	–	–	3
18	26	–	3	3	8	5	2	3	–	1	1	–	–	–	–	–	–	–
25	26	–	–	–	3	12	9	1	1	–	–	–	–	–	–	–	–	–
29	5	–	–	1	1	–	2	–	–	–	1^{1}	–	–	–	–	–	–	1
Sept. 1	2	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
13	5	–	1	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–

Table 4: Numbers of larvae per 100 litre low water plankton sample at Whitehouse Hole in the middle region of the river Roach during 1951. Small figures indicate eyed larvae in each size group.

Date	*Total larvae*	*Size distribution (mm.)*																*Total eyed*
		0·16	0·17	0·18	0·19	0·20	0·21	0·22	0·23	0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1951																		
June 7	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
14	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
18	69	–	2	17	32	16	2	–	–	–	–	–	–	–	–	–	–	–
21	144	–	10	45	29	44	10	4	–	2	–	–	–	–	–	–	–	–
25	163	–	19	49	65	20	10	–	–	–	–	–	–	–	–	–	–	–
28	748	–	66	237	362	72	11	–	–	–	–	–	–	–	–	–	–	–
July 2	1047	5	153	344	374	114	38	46	–	–	–	–	–	–	–	–	–	–
6	932	8	89	275	341	146	57	16	–	–	–	–	–	–	–	–	–	–
9	330	6	62	113	102	40	6	–	–	–	1^{1}	–	–	–	–	–	–	1
12	538	7	57	207	102	51	7	7	–	–	–	–	–	–	–	–	–	–
16	229	6	34	68	55	30	19	12	3	–	2^{2}	–	–	–	–	–	–	2
19	33	2	2	10	16	–	1	1	–	1^{1}	–	–	–	–	–	–	–	1
23	207	3	17	44	81	47	15	–	–	–	–	–	–	–	–	–	–	–
26	45	3	5	15	18	4	–	–	–	–	–	–	–	–	–	–	–	–
30	128	6	31	53	33	4	–	1	–	–	–	–	–	–	–	–	–	–
Aug. 2	213	16	62	37	39	37	11	11	–	–	–	–	–	–	–	–	–	–
6	48	–	6	20	18	4	–	–	–	–	–	–	–	–	–	–	–	–
9	40	1	7	14	8	7	2	1	–	–	–	–	–	–	–	–	–	–
13	298	6	93	146	41	2	–	–	–	–	–	–	–	–	–	–	–	–
16	70	4	10	20	13	13	4	4	–	–	2^{2}	–	–	–	–	–	–	2
21	34	All small except one eyed								1^{1}	–	–	–	–	–	–	–	1
30	100	All small none eyed																
Sept. 4	9	All small none eyed																

Table 5: Numbers of larvae per 100 litre plankton sample collected at low water at Burnham in 1951.

Date	*Total larvae*	*Size distribution (mm.)*															*Eyed larvae*
		0·16	0·17	0·18	0·19	0·20	0·21	0·22	0·23	0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1951																		
June 15	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19	3	–	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–
22	7	–	–	2	3	2	–	–	–	–	–	–	–	–	–	–	–	–
26	10	–	–	2	5	2	1	–	–	–	–	–	–	–	–	–	–	–
29	9	–	–	2	6	1	–	–	–	–	–	–	–	–	–	–	–	–
July 3	12	–	–	3	8	1	–	–	–	–	–	–	–	–	–	–	–	–
6	38	–	2	14	16	4	2	–	–	–	–	–	–	–	–	–	–	–
10	19	2	2	3	7	5	–	–	–	–	–	–	–	–	–	–	–	–
13	69	–	8	28	22	7	–	2	2	–	–	–	–	–	–	–	–	–
17	43	2	5	7	16	10	2	–	–	–	–	–	–	–	–	–	–	–
22	124	4	44	53	17	6	–	–	–	–	–	–	–	–	–	–	–	–
24	25	2	7	10	6	–	–	–	–	–	–	–	–	–	–	–	–	–
27	29	–	7	16	4	2	–	–	–	–	–	–	–	–	–	–	–	–
31	44	6	16	18	4	–	–	–	–	–	–	–	–	–	–	–	–	–
Aug. 3	25	–	8	14	3	–	–	–	–	–	–	–	–	–	–	–	–	–
7	61	3	5	30	20	3	–	–	–	–	–	–	–	–	–	–	–	–
10	45	–	11	12	7	10	3	2	–	–	–	–	–	–	–	–	–	–
14	37	3	8	17	7	–	1	1	–	–	–	–	–	–	–	–	–	–
22	7	All small less than 0·20																
29	18	All small 0·20 or less																

Table 6: Number of oyster larvae per 100 litre plankton sample collected at low water from the middle reaches of the river Roach at Whitehouse Hole in 1954. Small figures indicate numbers of eyed larvae in each group.

Date	*Total larvae*	*Size distribution (mm.)*															*Eyed larvae*
		0·16	0·17	0·18	0·19	0·20	0·21	0·22	0·23	0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1954																		
June 3	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	25	–	–	–	–	7	8	10	–	–	–	–	–	–	–	–	–	–
14	312	–	–	2	18	64	114	90	16	6	–	1	–	–	–	–	–	–
17	167	–	–	3	6	23	48	48	23	16	–	–	–	–	–	–	–	–
21	289	–	–	16	40	69	77	69	13	3	–	–	1^{1}	–	–	1^{1}	–	2
24	360	–	–	16	41	102	99	49	13	8	15	4	4	4	1^{1}	–	–	1
28	694	–	–	16	29	88	178	185	92	32	26	26	10^{6}	5^{5}	4^{4}	3^{3}	–	18
July 1	338	–	3	29	32	77	74	49	37	15	5	3	3^{3}	3^{3}	3^{3}	–	–	9
5	251	–	–	19	53	122	35	16	3	–	3	1^{1}	1^{1}	–	–	–	–	2
8	434	–	4	22	98	193	95	18	4	–	–	–	–	–	–	–	–	–
12	185	–	5	33	63	57	24	3	–	–	–	–	–	–	–	–	–	–
15	16	–	–	2	6	4	3	1	–	–	–	–	–	–	–	–	–	–
19	38	–	–	–	10	14	14	–	–	–	–	–	–	–	–	–	–	–
22	107	–	2	6	34	28	23	10	4	–	–	–	–	–	–	–	–	–
26	144	–	–	3	62	38	38	3	–	–	–	–	–	–	–	–	–	–
29	47	–	–	–	15	13	9	4	2	4	–	–	–	–	–	–	–	–
Aug. 3	41	–	–	5	7	20	7	2	–	–	–	–	–	–	–	–	–	–
5	109	–	2	5	9	27	39	19	8	–	–	–	–	–	–	–	–	–
9	136	–	–	4	16	44	47	21	4	–	–	–	–	–	–	–	–	–
12	20	–	–	–	3	4	7	5	1	–	–	–	–	–	–	–	–	–
16	14	–	2	4	5	3	–	–	–	–	–	–	–	–	–	–	–	–
19	24	–	2	3	5	9	3	2	–	–	–	–	–	–	–	–	–	–
23	44	–	–	2	16	13	8	5	–	–	–	–	–	–	–	–	–	–
26	2	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
30	3	–	–	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–
Sept. 2	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 7: Numbers of larvae per 100 litre sample at low water at Burnham during 1954. Small figures indicate numbers of eyed larvae.

Date	*Total larvae*	*Size distribution (mm.)*															*Eyed larvae*
		0·16	0·17	0·18	0·19	0·20	0·21	0·22	0·23	0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1954																		
June 1	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
11	7	–	–	–	–	–	2	2	3	–	–	–	–	–	–	–	–	–
15	76	–	–	–	1	32	29	9	4	–	–	–	–	–	1^{1}	–	–	1
18	135	–	2	4	5	29	45	36	9	3	–	1	–	1	–	–	–	–
22	218	–	–	7	16	50	76	38	19	7	1	2	–	1^{1}	1^{1}	–	–	2
25	721	–	3	6	58	178	158	137	96	45	19	13	6^{1}	1^{1}	–	–	–	2
29	307	–	–	8	25	45	65	74	25	25	8	–	8^{4}	9^{9}	4^{4}	1^{1}	–	18
July 2	221	–	–	6	61	51	59	19	16	3	–	3^{3}	3^{3}	–	–	–	–	6
6	141	–	3	7	32	56	28	11	–	–	3	1^{1}	–	–	–	–	–	1
9	366	–	11	37	83	121	58	33	11	8	4	–	–	–	–	–	–	–
13	8	–	1	1	4	2	–	–	–	–	–	–	–	–	–	–	–	–
16	56	–	–	14	26	12	–	4	–	–	–	–	–	–	–	–	–	–
20	48	–	–	9	21	9	5	3	–	1	–	–	–	–	–	–	–	–
23	95	–	–	2	24	41	19	7	–	1	–	1	–	–	–	–	–	–
27	84	–	5	7	9	23	16	11	4	2	5	–	1^{1}	–	–	1^{1}	–	2
30	8	–	–	–	1	3	1	2	1	–	–	–	–	–	–	–	–	–
Aug. 4	37	–	–	2	12	12	9	–	2	–	–	–	–	–	–	–	–	–
6	26	–	–	1	1	6	13	3	–	2	–	–	–	–	–	–	–	–
10	61	–	–	–	4	13	12	20	4	4	3	1	–	–	–	–	–	–
13	31	–	1	1	3	8	7	4	2	2	2	1	–	–	–	–	–	–
17	12	–	–	1	3	2	2	–	–	1	1	2^{1}	–	–	–	–	–	1
20	4	–	–	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–
24	5	–	–	–	1	1	1	2	–	–	–	–	–	–	–	–	–	–
27	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
31	6	–	–	–	1	1	2	2	–	–	–	–	–	–	–	–	–	–
Sept. 3	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–

Table 8: Showing numbers of oyster larvae in each of the smaller size groups and the size distribution of eyed larvae in the rivers Crouch and Roach, at monthly intervals during the five years. (*Continued on p. 24.*)

River Roach

Year and month	*No. of 100 litre samples*	*Total number of larvae in each size group (mm.)*						*Mean size (mm.)*	*Numbers of eyed larvae in each size group (mm.)*								*Mean size (mm.)*
		0·16	0·17	0·18	0·19	0·20	0·21		0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1950																	
June	24	1	101	314	605	1281	1412	0·200	-	8	21	51	103	49	23	–	0·279
July	27	69	252	679	1003	1186	670	0·193	7	51	49	36	27	7	1	–	0·263
Aug.	24	11	40	89	112	91	44	0·189	–	2	–	1	–	–	–	–	0·257
1951																	
June	15	8	199	699	933	309	65	0·187	–	–	–		–	–	–		
July	27	190	1608	3661	3295	1221	378	0·185	2	5	–	–	–	–	–	–	0·247
Aug.	21	79	472	687	407	159	49	0·181	2	2	–	–	–	–	–	–	0·245
1952																	
June	27	3	99	936	3404	6508	4131	0·199	–	–	1	21	17	24	9	–	0·283
July	27	59	355	1229	1612	1414	697	0·191		–	2	13	23	8	6	1	0·281
Aug.	21	6	37	106	163	81	17	0·188		–	–	–	–	1	–	–	0·290
1953																	
June	27	2	88	377	1141	1463	853	0·197	–		3	4	4	–	–	1	0·274
July	27	–	83	609	1548	1566	722	0·195	–	1	2	7	4	1	1	–	0·273
Aug.	27	–	32	270	608	316	163	0·192	–	–	5	3	–	–	–	–	0·264
1954																	
June	18	1	11	133	597	2188	2930	0·204	–	1	7	17	19	22	6	–	0·280
July	27	–	73	400	1085	1467	726	0·196	–	3	2	11	12	6	–	–	0·275
Aug.	27	–	10	59	227	390	255	0·199	–	1	–	4	–	–	-	-	0·260

Table 8 (Continued): Showing numbers of oyster larvae in each of the smaller size groups and the size distribution of eyed larvae in the rivers Crouch and Roach, at monthly intervals during the five years.

River Crouch

Year and month	*No. of 100 litre samples*	*Total number of larvae in each size group (mm.)*						*Mean size (mm.)*	*Numbers of eyed larvae in each size group (mm.)*								*Mean size (mm.)*
		0·16	0·17	0·18	0·19	0·20	0·21		0·24	0·25	0·26	0·27	0·28	0·29	0·30	0·31	
1950																	
June	21	16	107	244	649	1025	844	0·198	1	14	20	58	111	31	13	–	0·277
July	24	24	91	282	446	498	313	0·194	–	34	45	43	30	10	4	–	0·267
Aug.	24	23	82	182	311	285	186	0·192	–	22	11	8	2	–	–	–	0·258
1951																	
June	24	–	4	21	27	6	1	0·186	–	–	–	–	–	–	–	–	–
July	27	30	216	472	465	192	34	0·185	–	–	–	–	–	–	–	–	–
Aug.	31	20	83	157	79	22	9	0·181	–	–	–	–	–	–	–	–	–
1952																	
June	24	3	35	356	922	1954	767	0·197	–	–	–	–	–	–	–	–	–
July	27	8	28	223	638	851	512	0·197	–	–	5	9	7	–	3	–	0·275
Aug.	27	–	11	48	121	79	25	0·192	–	–	–	1	–	–	–	–	0·270
1953																	
June	27	–	4	67	246	375	266	0·199	–	–	–	–	–	–	–	–	–
July	30	–	10	145	406	438	187	0·196	–	1	2	1	1	1	–	–	0·268
Aug.	30	1	3	103	309	338	144	0·196	3	3	2	8	3	–	–	–	0·263
1954																	
June	28	4	12	80	295	911	1441	0·203	–	1	5	16	32	15	5	–	0·279
July	36	–	26	217	767	1029	668	0·198	1	3	5	14	10	1	1	–	0·270
Aug.	36	–	5	32	130	242	213	0·200	–	1	3	–	2	–	1	–	0·270

Knight-Jones (1952), who suggested that oysters which produce larvae late in the season have depleted food reserves, through earlier functioning as males.

The presence of paired eyes in the larvae indicates the approach of settlement and these eyes appear on smaller larvae at the end of the season than at the beginning. The implication is that those larvae which are initially big will grow to a larger size before developing eyes but it also seems possible that the age of the larvae has some bearing on this. In 1951 very few larvae grew and those only slowly (Tables 4 and 5). Eyed larvae were either 0·24 or 0·25 mm. in length. This suggests the operation of a time factor in that the larvae, having reached a certain age, were ripe for metamorphosis though they were below the normal size. Cole (1939) referred to a difference between the size of eyed larvae in the tanks at Conway (exceptionally 0·33 and 0·35 mm.) and in the Helford river (0·25 to 0·27 mm.) and concluded that '. . . . . under different conditions growth in size and differentiation of organs proceed at different rates . . . . .'. He also noted that the water temperature in the Helford river was 2-3°C. lower than at Conway though he did not suggest that higher temperatures could account for the larger eyed larvae. Knight-Jones did, however, suggest that there might be precocious development at higher temperatures, and that in colder water larvae would reach a larger size. He quotes Norris, Jones, Lovegrove and Crisp (1951), who found that barnacle larvae reared in colder conditions reached a larger size. Korringa (1941) also suggested more rapid development at higher temperatures. Both he and Knight-Jones stated that smaller eyed larvae appeared later in the season and were derived from larvae which were small at the time of liberation. From the present observations there is no evidence that low temperatures necessarily result in larger larvae; the summer of 1954 was cold, yet the size-distribution of the larvae was the same as in 1950 when the water was warm (Table 8). On the other hand more small eyed larvae appeared towards the end of 1950, presumably produced from late-spawning stock. If the effect of late spawning is to produce larvae with less food reserves, then there is an explanation for the size of the 1951 and 1953 eyed larvae. In 1951, as has already been stated, the oysters had been subjected to cold conditions and much lower salinities than normal. They were in poor condition and produced small larvae. In 1953 the stocks had been adversely affected by the floods early in the year and because of this, it is suggested, produced weakly larvae of small size. It is significant that, whereas the normal size of the eyed larvae is of the order of 0·27 mm. in the Crouch and Roach, the mean in 1951 was 0·25 mm. and in 1953 0·26 mm. (Table 8). The mean size of the larvae at liberation was also smaller in these two years. A further consideration in connection with this production of small larvae is the possibility that they will produce stunted spat which in turn may produce stunted though mature oysters (Cole and Waugh, in preparation). Certainly local oystermen believe that a June spat is worth more than an August one. They say the June spat grows well before the winter and in the following year will reach good proportions,whilst the August one will remain stunted. The June spat, i.e., the first spat of the season, are, as has been shown, derived from a larger, stronger stock of larvae than the August ones.

The duration of the planktonic stage is normally 8 to 10 days but is increased by low temperatures. Korringa (1941) showed that the pelagic stage varied from approximately 6 days at 22–23°C. to 14 days at 16–17°C.

In 1950 newly liberated larvae were present in the water in the river Roach on June 6 and by June 12 there were already eyed larvae in the water, indicating a planktonic life to the eyed stage of approximately 7 days at a mean water temperature of 21°C. Subsequent liberations were not easy to follow but it appeared that many of the eyed larvae present in the sample of July 17 were derived from those liberated on July 10, indicating a larval life to the eyed stage of 8 days at the most, at a temperature of approximately 20°C. (Table 2). In the river Crouch on June 5 there were no larvae, on June 8 the total number of larvae obtained from the three sampling stations was only 18 but by June 13 the total was 719 with 17 eyed larvae. These eyed larvae must have been derived from larvae liberated on or about June 8, which indicates a larval life to the eyed stage of approximately 6 days. No temperatures were taken in the Crouch in that year but subsequent experience suggests that they would have been 1°C. higher than in the river Roach. Development therefore took place at about 22°C.

It is difficult to draw conclusions about the rate of development in 1951, though the few larvae which did reach the eyed stage probably took 11 days, from June 28 to July 9, to develop at a temperature of approximately 19°C. (Table 4). However, very heavy losses of the larvae (560 empty paired larval valves were counted together with the 1,299 living larvae in the Roach Mouth sample of July 2) made it virtually impossible to make an accurate assessment.

Larval liberations for 1952 and 1953 are not tabulated, but it was concluded that in 1952 one batch took at least 10 days to reach the eyed stage at a temperature of 17°C. and another approximately 8 days at 19°C. In 1953 one batch developed to the eyed stage in 7 days at 20°C. In 1954 (Table 6) larvae liberated between June 10 and June 14 became eyed between June 21 and June 24, i.e., 10–11 days at ca. 17°C.

Summarising: development to the eyed stage took 7 days at 21°C. and 6 days at 22°C. in 1950; 11 days at 19°C. in 1951; 8 days at 19 °C. in 1952 and 1953 and 11 days at 17°C. in 1954. There is good agreement with Korringa who concluded that the length of the pelagic stage was largely dependent on water temperature and that Cole had underestimated its influence when he suggested that the lengthening of the free swimming period

Table 9: Showing mean numbers of newly liberated larvae, less than 0·22 mm. in length, and mean numbers of actively growing larvae more than 0·24 mm. in length, per 100 litre sample at stations in the rivers Crouch and Roach.

The percentage of liberated larvae which were actively growing is also shown. (In 1951, though some did reach more than 0·24 mm. they could not be considered as growing actively.) In addition, percentage surviving to settlement size is shown.

Station	(*a*) < 0·22 *mm.*	(*b*) > 0·24 *mm.*	(*c*) *eyed*	(*b*) *as %* *of* (*a*)	(*c*) *as %* *of* (*a*)
1950					
Paglesham	36·3	5·85	2·52	16·1	6·9
Whitehouse Hole	134·9	20·18	7·52	15·0	5·6
Roach Mouth	136·4	16·76	6·60	12·3	4·8
Burnham	56·3	9·44	5·08	16·8	9·0
Althorne	73·2	12·76	6·36	17·4	8·7
Ray Pits	96·3	16·52	6·92	17·2	7·2
1951					
Paglesham	95·0	0·09	0·05	0·1	0·05
Whitehouse Hole	238·1	0·23	0·32	0·1	0·13
Roach Mouth	359·1	0·09	0·14	0·03	0·04
Burnham	32·5	0·00	0·00	0·00	0·00
Althorne	32·9	0·00	0·00	0·00	0·00
Ray Pits	29·3	0·00	0·00	0·00	0·00
1952					
Paglesham	103·4	4·26	0·93	4·1	0·9
Whitehouse Hole	319·2	8·46	1·85	2·7	0·6
Roach Mouth	367·6	12·41	1·96	3·4	0·5
Burnham	105·1	1·52	0·48	1·4	0·5
Althorne	72·4	0·59	0·15	0·8	0·2
Ray Pits	66·3	1·00	0·33	1·5	0·5
1953					
Paglesham	57·4	0·68	0·16	1·2	0·3
Whitehouse Hole	141·0	0·77	0·15	0·5	0·1
Roach Mouth	182·2	2·23	1·08	1·2	0·6
Burnham	45·5	0·54	0·31	1·2	0·7
Althorne	31·7	0·42	0·19	1·3	0·6
Ray Pits	23·3	0·50	0·31	2·1	1·3
1954					
Paglesham	150·3	4·58	1·54	3·0	1·0
Whitehouse Hole	114·7	5·29	1·33	4·6	1·2
Roach Mouth	174·8	8·63	1·75	4·9	1·0
Branklet	76·0	8·04	2·00	10·6	2·6
Burnham	70·6	4·19	1·27	5·9	1·8
Althorne	54·4	2·42	0·81	4·4	1·5
Ray Pits	29·6	2·42	0·42	8·2	1·4

by water temperatures as low as 15–17°C. was not likely to exceed one day or at the most two. However, Cole, who suggested that the abundance of food was more likely to be the limiting factor, was probably partially correct as evidenced by the slow development of the 1951 larvae which, though living at a moderate temperature, were short of food. It seems that the two are interrelated and that temperature is the dominant factor. Certainly the feeding rate of the larvae increases with increasing temperature (Drinnan, personal communication) and presumably the rate of development also, provided food is adequate. It was only in 1951 that food supply seemed insufficient to permit growth and development (Waugh 1952).

Whilst survival of the larvae to settlement is dependent on food, enormous numbers must be lost during development as a result of predation by *Sagitta*, *Ascidiella*, *Ciona* and *Polydora* (Cerruti 1942). Observations made by Mr. Shelbourne during 1951 and 1952 showed that *Aurelia aurita* and *Pleurobrachia pileus* also consume vast quantities of larvae and are probably the most important predators in the two rivers (see also Orton 1922). The more rapid the development to settlement size the less chance there is of these predators taking their toll. A higher proportion of eyed larvae would, therefore, be expected in a season of rapid growth. The percentages of larvae reaching the eyed stage in 1947, 1948 and 1949 were approximately 1, 8 and 5 respectively (Knight-Jones 1952). The present results show more variation (Table 9). In 1950 7% reached the eyed stage, in 1951 only 0·04%, in 1952 0·5% and in 1953 0·6%. In 1954, despite slow development, 1·5% became eyed.

Table 8 gives the size-distribution of small larvae (freshly liberated) and of eyed larvae derived by summing the results of all pump samples at monthly intervals. From these the mean size at liberation and during the eyed stage has been calculated. The results, presented graphically in Fig. 13, show that the size of the eyed larvae was governed by the size at liberation. Except in 1954 the mean size of the freshly liberated and the eyed larvae decreased as the seasons progressed. In that year the low summer temperatures may have delayed liberation or limited production of larvae so that those produced had bigger food reserves. In 1950, when the larvae were also large, temperature conditions were completely different but in both seasons the oysters were in good condition and presumably because

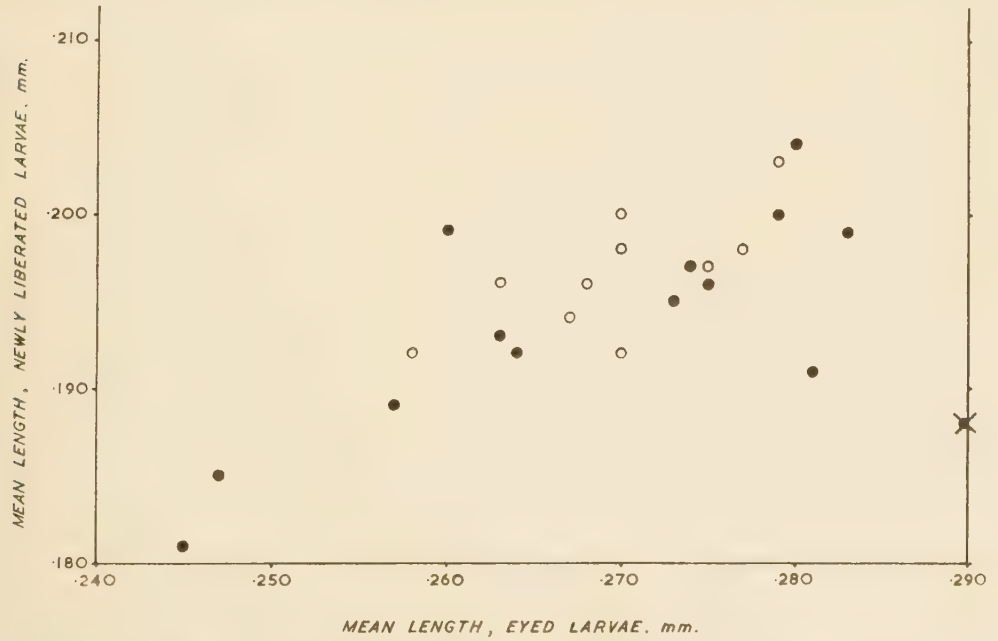

Fig. 13. *Showing the relation between the size at liberation and the size of the eyed stage amongst larvae in the river Crouch (open circles) and river Roach (solid circles). X is from a single observation.*

of their extra food reserves, produced bigger stronger larvae. On this basis, it is suggested that had the 1954 season been warmer the spatfall would have been good, whereas in 1951, even if the summer had been exceptionally good, spatfall would have remained meagre.

Other causes of loss of larvae are slow development, resulting in an increase in the area over which they are dispersed, and changes in water movement, which also result in more rapid dispersion. For example, as shown in Section VII, excessive rainfall causes displacement of river water out to sea and prolonged strong winds can also cause abnormal mixing of river and sea water.

IX. DISTRIBUTION OF BREEDING STOCKS

Knight-Jones (1952) described the general distribution of the stocks of mature oysters in the rivers Crouch and Roach up to 1949 and Shelbourne (In press) has since described, in more detail, the results of a survey made in 1951. After that time there was comparatively

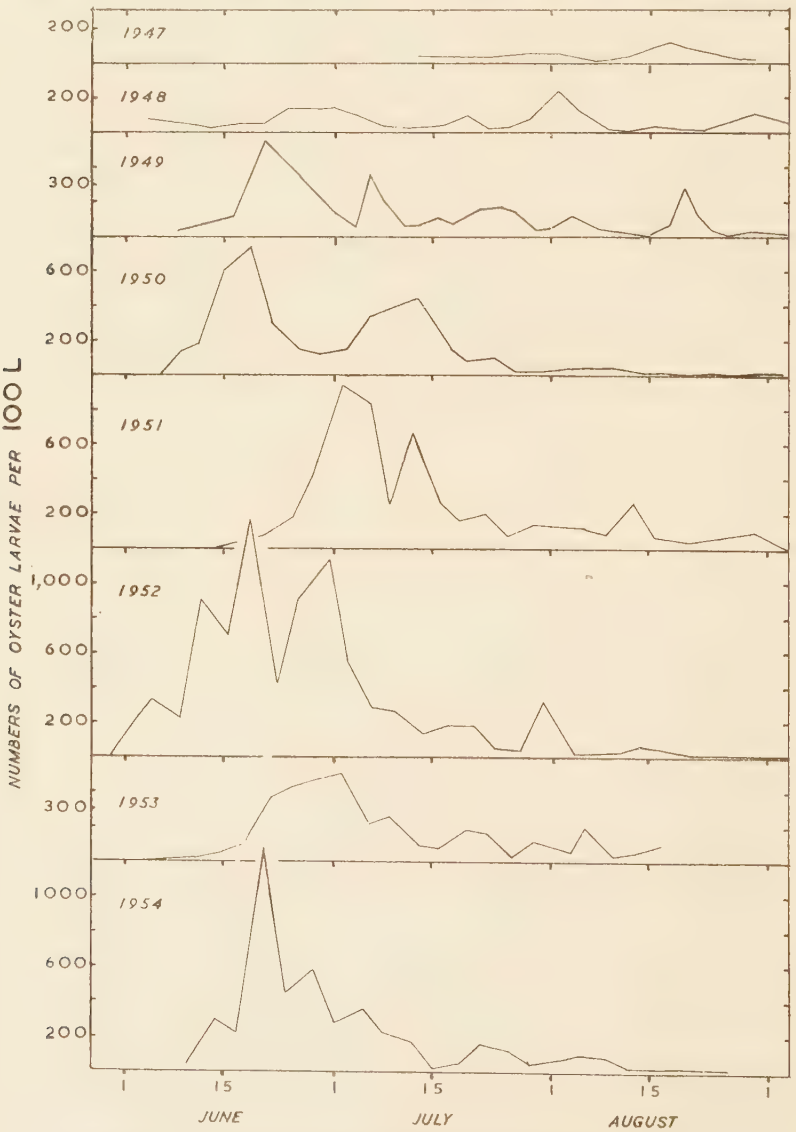

Fig. 14. *Annual production of oyster larvae in the river Roach since* 1947.

little restocking of the two rivers except in the Paglesham area where approximately 250,000 young oysters were laid by the Ministry and the oystermen. Except here, the distribution varied little from that described by Shelbourne, until the 1953 flood. The result of this was to cause heavy losses in the upper Crouch and in the creeks of the river Roach. In the Paglesham area the mortalities though high, were fairly uniform (25–30%), so that the distribution pattern in the Roach still remained the same in that the biggest percentage of mature oysters was still in the Paglesham area. In the river Crouch the heaviest concentrations were from the middle reaches to just below Burnham.

The general policy of the oyster farmers has maintained this distribution, as young oysters from the upper part of each river are dredged up and relaid down-stream in deeper water where they are less exposed to the effects of reduced salinity and extreme cold. The reason why the lower reaches of the river Roach are not used will be explained later (page 42) but Paglesham Reach itself supplies an adequate deep water laying.

Allowing for fluctuations in the numbers of larvae produced by each oyster, due to varying seasonal conditions and the percentage functioning as females, it is still reasonable to consider total production of larvae as being, in part, a measure of the abundance of breeding stocks. In the river Roach, particularly, there was a steady increase in the quantity of larvae produced each season up to 1953 and it is considered that this reflects the quite intense restocking that had been carried out. The abrupt drop in 1953 was probably due to the considerable reduction of stocks brought about by the floods (Fig. 14). Restocking of the river Crouch was much less intense but in this river too a similar trend was observed. The reduction in 1951 was probably due to the losses of stock in the preceding winter and to exceptional dispersion of larvae which resulted in many being missed by the sampling technique used (see page 10).

X. DISTRIBUTION AND INTENSITY OF SPATFALL

To assess the distribution and intensity of spatfall, smooth slates were exposed for weekly intervals, just below low water of spring tides, at various places in the two rivers. The slates, either singly or in pairs, were held horizontally about 5 cm. above the surface of concrete blocks (for detailed description see Knight-Jones 1952). The slates used measured 25 × 18 cm.; for laboratory counts a squared grid was used which covered a central area of 212 cm^2. As both upper and lower surfaces were examined, the effective area counted on each slate was 424 cm^2.

In mid July 1954 their use was discontinued. The periods of exposure of the slates and the numbers of spat observed on them up to that time are shown in Fig. 15. Slates were abandoned because it was felt that they did not give a true picture of the spatfall. A most striking example occurred in 1950. The concrete block supporting the Fambridge slates was lifted on October 27 and was found to bear 284 well-grown and 51 recently dead spat. This block, approximately 4 times the surface area of a slate, bore approximately 12 times as many living spat as had been recorded on the slates changed at weekly intervals and approximately 10 times as many as on the slate left down permanently. The total recorded represents only that portion of the spatfall which survived and grew after metamorphosis. The actual number setting was probably much greater, for spat dying at one or two millimeters length leave little or no trace after two or three months. The Purleigh Shore block, too, bore 83 live and 43 recently dead; as opposed to 68 recorded on the weekly changed slates and only 1 on the unchanged one. This again indicated a heavier spatfall than expected. From these and other observations it appeared that the slates might be unreliable, perhaps because they presented a smoother, more exposed, surface for attachment. The blocks may have been more suitable because they were slightly fouled and so more attractive to spat (Cole and Knight-Jones 1939 and 1949) but the same effect should have been seen on the slates left down permanently.

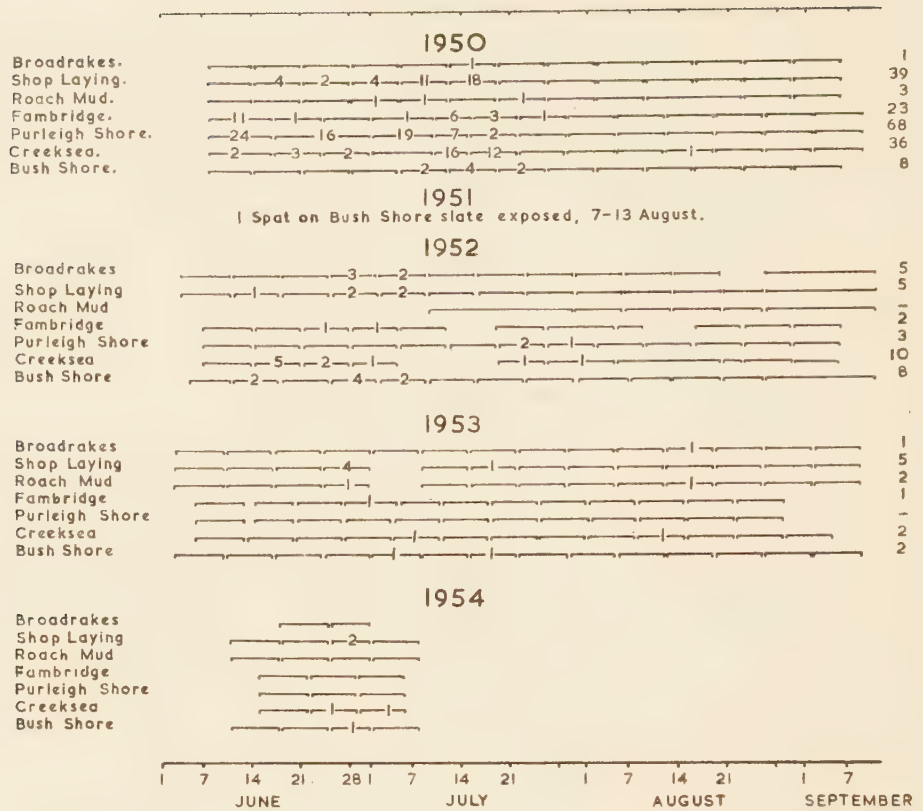

Fig. 15. *Oyster spatfall on slates at various localities during the five years. Numbers of spat on each slate are shown by figures and the length of the lines indicates the period of exposure of the slates.*

Another drawback, particularly evident in 1951, was that the slates were often smothered on the underside by the eggs of *Gobius minutus*. Such a slate provided no surface, or very little, to which either barnacle cyprids or oyster larvae could attach and, even after vigorous scrubbing, enough bases of the egg capsules were left to interfere with settlement. Characteristic barnacle-free areas occurred on such slates after re-exposure.

Settlement of *Elminius modestus* on the slates increased year by year so that less surface was available for spat settlement. This resulted not only from the increasing population of barnacles on the grounds as a whole, but also from gregarious setting (Knight-Jones and Stephenson 1950). This phenomenon has since been described in other marine animals by Knight-Jones (1951 and 1953), who has shown that the remains of bases of sedentary animals act as attractants for larvae of their own species. It was therefore expected that recolonisation of the cleaned re-used slates, by *Elminius*, would be more rapid than if new ones had been used each time, but the rate of setting of the barnacle is now so high that this effect was obscured (Section XII).

Spatfall, as recorded on the weekly changed slates, showed limited correlation with the numbers of eyed oyster larvae in the water. Eyed larvae averaged 1·56 per 100 litres in the river Crouch in 1948 (Knight-Jones 1952) and the spatfall on the slates was 155. In 1949 eyed larvae averaged 1·1 per 100 litres and spatfall on the slates totalled only 52 though some slates were lost that season. In 1950, when eyed larvae averaged 6·12 per 100 litres, the spat on the slates was only 129. It would seem that either the slates were becoming less suitable as collectors or that, in 1948, oyster spatfall on them was abnormal. Knight-Jones, although he referred to the greater crowding of the slates by *Elminius* in 1949, took the view that the apparently abnormal 1948 spatfall on slates was cataclysmic and that the gregarious tendency affected large numbers of eyed larvae immediately after the attachment of the few. Such an argument does not hold good for 1950 when eyed larvae at any one time were twice

*Table 10: Showing numbers of spat which settled on slates throughout each season, the numbers counted on 10 clocks after peak settlement and the average number per egg-box collector, in the 5 seasons. Mean numbers of eyed larvae per 100 litres in each river are also shown. The additional number of eyed larvae for the Crouch in 1954 includes the Branklet samples. – indicates no observation, *indicates a low value, because collectors were set out after peak settlement.*

		Crouch						*Roach*					
		Fambridge	*Purleigh*	*Black Point*	*Creeksea*	*Bush Shore*	*Mean*	*Broadrakes*	*Common Shore*	*Shop Laying*	*Roach Mud*	*Roach Mouth*	*Mean*
1950	Slates	24	68	–	37	8	34	1	–	39	3	–	14
	Clocks	210	106	–	257	12	146	–	–	138	–	–	138
	Collector	–	22*	–	–	–	22*	–	110*	270*	–	–	190*
	Eyed larvae						6·12						5·70
1951	Slates	0	0	–	0	1	0·25	0	0	0	0	–	0·0
	Clocks	0	–	–	0	0	0	–	0	0	–	–	0
	Collector	0	0·4	–	–	–	0·2	0·1	1·4	–	–	15	4
	Eyed larvae						0·0						0·13
1952	Slates	2	3	–	10	8	5·8	5	–	5	0	–	3·3
	Clocks	4	0·5	–	46	–	16·8	–	17	34	–	–	25
	Collector	6	15	21	–	–	14	18	–	175	–	32	75
	Eyed larvae						0·32						1·60
1953	Slates	1	0	–	2	2	1·3	1	–	5	2	–	2·7
	Clocks	7	–	–	83	198	96	7	–	56	–	–	21
	Collector	35	40	53	–	–	43	–	90	75	–	80	81
	Eyed larvae						0·26						0·46
1954	Slates	–	–	–	–	–	–	–	–	–	–	–	–
	Clocks	12	24	–	10	41	22	26	4	45	–	–	25
	Collector	55	74	147	–	–	92	25	129	24	–	132	78
	Eyed larvae						1·13 0·83						1·54

as abundant as in 1948 though the settlement on the slates was less. It seemed that the increasing barnacle settlement had a proportionately greater effect each year in reducing the surface area available for oyster spat.

Unsatisfactory results such as these led to the conclusion that a more accurate assessment of oyster spatfall could be made by examining clocks (i.e. oyster shells where the two valves remain hinged) and egg-box collectors. Neither of these methods is completely satisfactory as they record only those spat which have settled and survived. Shells were usually examined 1–2 weeks after the main settlement; collectors, except in 1950, were broken up at the end of each season and the spat carefully counted. To provide comparable data, slates, clocks and collectors were examined each season until 1954; the results are shown in Table 10.

In 1950, the spat on shells averaged 144 per ten clocks; a considerable increase on the 85 recorded by Knight-Jones in 1948. This was the first spatfall, at the conclusion of which the clocks were examined. Egg-boxes on Shop Laying and Common Shore were not broken up until the following spring, when they yielded an average of 270 and 110 spat per collector; the initial spatfall on them must have been much greater. On Purleigh Shore additional egg-boxes were put out in August in time to record the second spatfall.

Settlement on the slates indicated a more intense spatfall in the lower Crouch whereas the spatfall on shells was greater in the upper Crouch where the oyster larvae were most abundant (page 14).

In 1951 collectors were exposed at many more places and a better picture of spatfall was obtained. Settlement was practically nil in the upper reaches of the two rivers and very limited at Roach Mouth. No spat were observed on clocks and the only one found on the slates was at Bush Shore. Generally this picture of settlement accorded well with the results of plankton sampling.

In 1952 spatfall on both clocks and collectors was light and correlated with the numbers of eyed larvae in the plankton, but in 1953, though eyed larvae were few, spatfall was more dense than expected. In 1954, though eyed larvae were much more plentiful, spatfall appeared to be of the same order as in 1953.

The causes of the apparent anomaly observed in 1953 were investigated. One possible error lay in the technique used for sampling and in 1954 particular care was taken to ensure that no losses of larvae could occur through faults in either the pump or nets.

Table 11*: Showing the high proportion of larvae present in the Branklet samples at the end of* 1953.

Date	*Nos. of larvae per* 100 *litres in* 1953			
	Ray Pits	*Althorne Creek*	*Burnham*	*Branklet*
August				
11	28	11	47	12
14	14	4	71	278
18	10	45	32	237
21	9	34	16	30

There is no evidence, from the size distribution and abundance of the larvae in the two years, to indicate that the 1953 samples were at all unusual but there was a possibility that a true cross-section of the larval population was not being obtained. Reference has already been made to a possible movement of larvae downstream in the Crouch as a reason for including the Branklet station (page 10). The first observations there were made in 1953, unfortunately too late in the season to obtain eyed larvae, but as shown in Table 11 there was a markedly greater larval population at low tide than at the other stations further upstream. Similar results were obtained in 1954 (Table 9). However, discounting the

Branklet samples, eyed larvae were less than $\frac{1}{3}$ as abundant in 1953 as they were in 1954. Conditions of wind and tide could have contributed to the unusual settlement but the most important factor was the much improved state of cultivation of the Creeksea and Bush Shore grounds on which there was a heavier than normal spat which weighted the season's results. In particular on Bush Shore 100,000 oysters had been laid in May, June and July 1953 and the ground was much cleaner than it had been previously, so that in this season, when because of the storm surge in January, silt still lay over large areas of river bed,there were patches of clean well-stocked ground suitable for spatfall. Notes were made in 1953 of the difficulty of selecting suitable clocks because so many were fouled with silt and encrusting growths. It was only at Creeksea and Bush Shore that clean clocks were common and these areas were probably heavily colonised by spat simply because they were the only grounds in a suitable condition for settlement. Egg-box collectors which presented clean silt-free surfaces, in a season when they were not so common as usual, naturally collected a rather heavy settlement. These occurrences are in line with Knight-Jones' observations that slates on heavily stocked ground collected proportionately far fewer oyster spat than those on barren grounds. He suggested that on stocked ground, because of gregariousness, the spat settled on and amongst the oysters rather than on the collectors, and on barren ground they settled on the only available clean surfaces. Anomalous spatfalls also occurred in Holland in 1953 and these too were attributed to turbulent weather and high concentrations of silt (Korringa 1953).

It is apparent that estimations of spatfall, by whatever means, are likely to be misleading unless due consideration is given to the cleanliness of the test surfaces, the amount and distribution of additional settling surfaces, the state of cultivation and abundance of oysters in their immediate vicinity and the abundance and distribution of larvae, about to settle, in the plankton.

The general picture obtained from all the results was of a moderate settlement of oyster spat in 1950, little or none in 1951, very slight in 1952, light but localised in 1953 and light in 1954.

XI. WINTER MORTALITIES

In the shallow Essex rivers rapid reductions in water temperature occur in cold weather and prolonged rainfall results in an appreciable drop in salinity. Low temperature, alone, causes few losses, unless the oysters are exposed on the shore to freezing conditions, but reduced salinity may cause heavy mortalities, particularly if it is associated with low temperature.

In 1950 although no detailed survey was made, it was noted that there were few recently dead oysters. Mortalities during the succeeding four years are shown in Table 12. Those of 1950-51 and 1952-53 were heavy, particularly the latter. Generally, mortalities were heavier in the river Crouch than in the Roach. The catchment area of the former is much larger so that the effects of prolonged rainfall in reducing salinity are more severe, particularly in the upper reaches, where losses have always been heaviest.

There was little doubt that reduced salinity was responsible for the losses that occurred in the winter of 1950–51 (see page 4). There was a gradation from a mortality of 57% at Brandy Hole, in the upper Crouch, to 6% at Bush Shore in the lower part of the river. Water temperature, alone, could not have accounted for the mortalities, as it did not fall below 0°C. at any time and was below 3°C. for only 29 days in the whole period from November 1, 1950 to March 31, 1951. Temperatures below the limit of effective ciliary action, 5°C., occurred on 94 days in the same period.

In contrast, the winter of 1951–52 was comparatively dry and the lowest salinity recorded at Fambridge was 21‰ on March 17. Mortality was light; temperatures reached somewhat lower levels than in 1950–51 but the cold did not persist. Temperatures below 0 C. were recorded on 3 days in February, 1952; temperatures below 3°C. occurred on 34 days and below 5°C. on 71 days. The main difference between the two winters lay in the salinities.

Table 12: Showing the percentage mortality amongst oysters of all ages at the end of each winter at various stations in the rivers Crouch and Roach. Mortalities during the winter of 1949–50 were light on all grounds.

Station	1950–51	1951–52	1952–53	1953–54
River Crouch	%	%	%	%
Brandy Hole	57	1	95	29
Fambridge	40	5	57	10
Purleigh	30	7	51	13
Creeksea	2	2	24	8
Bush Shore	6	6	19	–
River Roach				
Broadrakes	7	3	22	–
Common Shore	4	4	–	–
Shop Laying	20	4	38	<10
Paglesham Reach	15	6	35	<10

In 1953 heavy mortalities in many localities were brought about by the floods (Waugh 1954b) but it was expected that losses would, in any case, have been fairly heavy, because of the poor condition of the oysters at the end of the summer and the very prolonged though not particularly cold winter. Although water temperatures did not fall below 0°C., values below 3°C. were recorded on 77 days, and below 5°C. on 119 days, during the season. Thus there was a cold period of almost twice the length of those experienced in the two previous years. No records of salinity are available from Fambridge during February and early March, 1953, but from rainfall records and earlier salinity observations it appeared unlikely that the salinity fell as low as 20‰ for more than 3 or 4 days. However, in the upper Crouch the very prolonged cold weather, acting on oysters that were already weak at the beginning of the season, would probably have resulted in substantial losses and in these circumstances the extreme turbidity brought about by the flood caused very heavy mortalities.

During the winter of 1953–54 there was a short spell of very cold weather in early February when ice formed on both rivers. Temperatures of 0°C. and below persisted for 13 days and ice was present for 9 days. Temperatures remained below 3°C. for 44 days and below 5°C. for 63 days. Freezing conditions occurred at spring tides but the ebbs were poor and few oysters were exposed on the shore to extreme cold. When the thaw set in, although salinities dropped abruptly, water temperatures rose rapidly so that the combined effects of cold and low salinity were minimised. In early March there was a moderate snowfall and fairly heavy rain which once again reduced salinity. These reductions were probably responsible for most of the losses that occurred.

Relaying of oysters was practised throughout the five years. In 1949 and 1950 substantial numbers of Conway tank-bred oysters were laid in the Crouch and Roach. They did not grow and fatten satisfactorily though they have done so elsewhere. When the Fambridge-Purleigh Shore stretch of the Crouch was surveyed in April 1951, it was found that between 94 and 95% of the Conway oysters still remaining on the grounds were dead. Mortality amongst native oysters was 40 to 42%. These mortalities were caused by the preceding winter conditions. In Paglesham Reach losses of relaid Brittany oysters in 1953 amounted to 40% and of natives to 30%. Fal oysters laid on this ground in October 1952 had suffered a 98% mortality. There is little doubt that the native spatted oyster is better suited to resist adverse conditions than those introduced from elsewhere. As a great many of the 'native' oysters are derived from spat produced by relaid Brittany and other oysters, it would appear that their resistance is dependent on their being reared in a given locality (Orton 1940). Certainly spat are more resistant than older oysters. In 1951 mortality of oysters over 1 year old was approximately 30% above that of spat less than 1 year old.

Transplantation of oysters from a locality where the water is very turbid or cold to a situation where the water is warmer or less turbid is likely to meet with more success than transplantation in the reverse direction, though 'native' oysters can be reared to maturity

quite successfully on their own ground, unless spatted in the extreme head-waters of the river where they may be killed in wet or cold winters (see Walne 1956).

All surveys and assessments of mortality were made either at the end of March or in early April when the water temperatures were between 6° and 8°C., because it had been found that losses due to adverse winter conditions do not become apparent until after temperatures are suitable for feeding. Even in 1951 and 1953, when conditions were particularly unfavourable early in the year, the mortalities did not reach a high level until the Spring.

XII. SETTING OF *ELMINIUS MODESTUS*

This barnacle was first recorded in the Crouch-Roach river system in 1945 by Crisp and Chipperfield (1948). Knight-Jones (1952) showed that the population had steadily increased during the period up to and including 1949. In 1950, a season particularly suited to the development of the larvae of many sedentary filter feeders, settlement was still more intense. Fig. 16 shows that in the river Roach the rate of settlement had reached a more or less steady level by 1953 but that in the river Crouch it was still increasing, particularly on Bush Shore. The peak density observed was on this ground in 1953 when 49,000 barnacles were recorded on the underside of a slate exposed from June 17–24. This density of approximately 230 per cm.^{2} was very considerably in excess of the peak of 90 per cm.^{2} recorded in 1949 by Knight-Jones.

The stable population in the river Roach and the increasing population in the river Crouch can be explained on the basis of the different levels of cultivation on the Ministry's grounds in these two rivers. In the river Roach, Shop Laying, our main stock ground for oysters, had been maintained in essentially the same state of cultivation throughout the period and the Roach Mud region, by its very nature, had also remained unchanged. In 1952 and 1953 the state of the Broadrakes ground was improved slightly by removal of old cultch from one part but it too had remained in essentially the same state of cultivation from the point of view of abundance of oysters and shells.

In the river Crouch, on the other hand, the area reclaimed on the Ministry's grounds had been increased and the state of cultivation of all four layings improved each year. Mistakidis (1951) suggested that reclamation of a ground, involving the addition of new cultch and the dredging up of buried shell, would result in a general increase in the numbers of sedentary organisms '. . . . such as *Elminius modestus*'. The increasing settlement of the barnacle in the Crouch, as cultivation improved, supports this view.

The differences in intensity of settlement from ground to ground were well defined. The exceptionally high density on Bush Shore may result from the high turbidity of the water in this region. Mistakidis (1951) referred to this as an explanation for the scarcity or absence of some of the more typical filter feeding organisms, such as ascidians and sponges, which were better represented in the cleaner waters of the river Roach. Moore (1944) described *Elminius modestus* as typical of quiet muddy estuaries and commoner in turbid water than other species of New Zealand barnacles. Though water movement in the river Crouch is fairly rapid, the flow over Bush Shore is less than in mid river (Shelbourne, In press). Reduction in flow alone cannot account for the high rate of settlement, because in the Black Point, Althorne Creek and Fambridge regions, where flow is also reduced, settlement of *Elminius* is less. In none of these places is the rate of flow and, therefore, the shear at settlement surfaces, so low as to prevent the settlement of the barnacle (Crisp 1955). It is more probable that the extreme turbidity of the water at Bush Shore favours *Elminius* in some way; either because it is particularly well adapted to muddy conditions or because it is unable to compete effectively in clearer waters with other sedentary animals, e.g., ascidians.

Elminius has been present in the Helford river in Cornwall since 1947 (Knight-Jones 1948) and I have observed it there since 1952. It is far less abundant in these clear waters

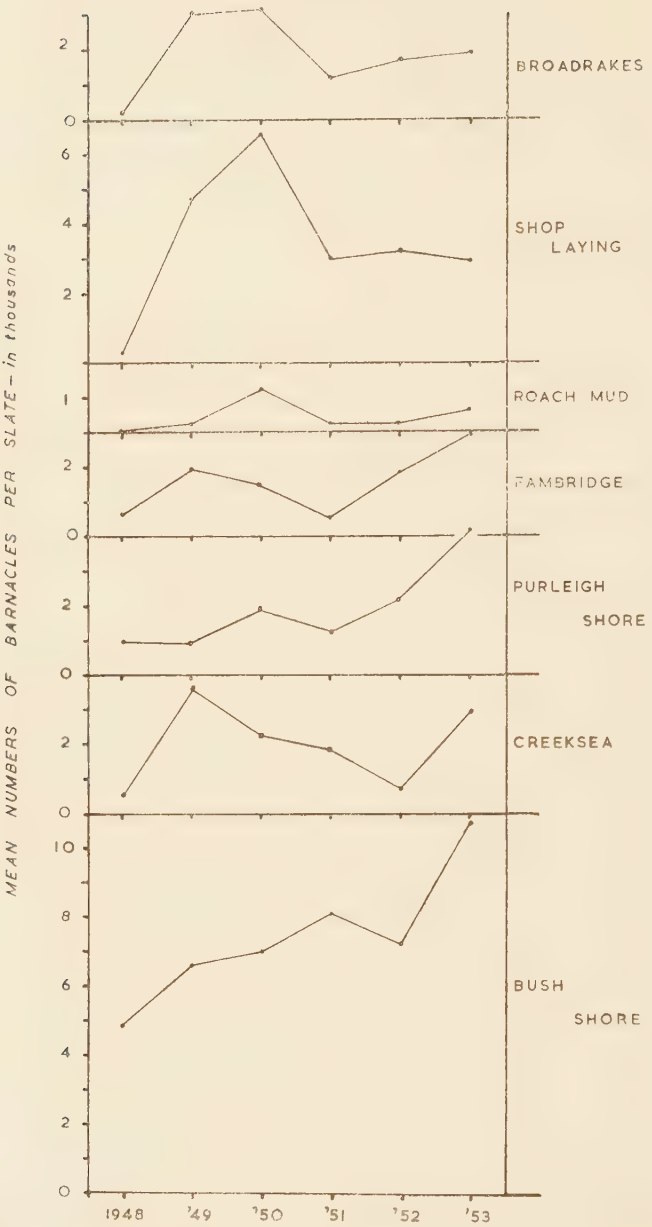

Fig. 16. *Showing mean numbers of barnacles which settled each season on the slates changed at weekly intervals.*

and the population has not increased with the same rapidity as it has in Essex, though the individual barnacles, perhaps because they are less crowded, are much larger. It is more common in the muddy creeks than in the main channel of the Helford river. It appears, therefore, that turbidity rather than water flow is the important factor governing its distribution and abundance.

In Essex *Elminius* occurs from approximately high water of neap tides to just below low water of spring tides. In the lower part of its range it competes with *Balanus improvisus*, which extends from well below low water up to approximately low water of ordinary tides. Whilst *Elminius* is unlikely to oust *Balanus improvisus* completely, it may replace it on the lower shore. From the results of the examination of slates, left down for the whole season

in 1951, 1952 and 1953 (Table 13), it appears that such a replacement is occurring. Single specimens of *B. improvisus* on the slates were often so far apart (6 to 10 cm.) that cross fertilisation would not have been possible. The nauplii closely resemble those of *Elminius* (Knight-Jones and Waugh 1949) and must experience severe competition in their search for food.

Table 13*: Showing* Elminius *as a percentage of total barnacle settlement* (Elminius modestus + Balanus improvisus) *present on slates after exposure for the whole of the summer seasons of* 1951, 1952 *and* 1953

Station		*Percentages of* Elminius *on slates exposed for whole summer season*		
		1951	1952	1953
Purleigh Shore	Top	74·5%	94·0%	99·7%
	Bottom	74·7%	86·0%	99·7%
Fambridge	Top	99·7%	–	–
	Bottom	99·9%	–	–
Bush Shore	Top	76·0%	100·0%	100·0%
	Bottom	95·7%	99·8%	100·0%
Broadrakes	Top	83·0%	100·0%	93·3%
	Bottom	97·0%	100·0%	91·3%
Shop Laying	Top	–	99·5%	99·5%
	Bottom	–	100·0%	99·5%

XIII. SETTLEMENT OF OTHER SEDENTARY ORGANISMS

The commonest animals settling on the slates were *Elminius modestus*, *Crepidula fornicata* and *Ostrea edulis*, the last two at approximately the same frequency. Other species occurred less often. The most common were gastropod post-larvae, particularly *Littorina littorea;* lamellibranch post-larvae, e.g., *Cardium exiguum* and *Mytilus edulis;* bryozoan colonies of *Scrupocellaria scruposa* and *Bicellaria ciliata* and the ascidian *Dendrodoa grossularia.* Foraminifera, amphipods, ostracods, copepods and polychaetes were also observed, mainly in the layer of silt which was frequently found on the upper surfaces of the slates.

Dendrodoa grossularia was only recorded infrequently despite its abundance on some of the oyster grounds, notably Fambridge. Even in 1950, a favourable season, it did not appear in quantity on the slates, though Knight-Jones recorded totals of 170 and 90 in 1948 and 1949 respectively. Details of the settlement and abundance of the organisms recorded are given in Table 14. It appeared that *Dendrodoa* was decreasing in abundance though no evidence of this was seen on the grounds.

Knight-Jones (1951b and 1952) found that certain species favoured either the upper or the lower surfaces of the slates. The settlement observed in the five years covered in this report was generally so light that firm preferences could not be established, though *Bryozoans* and oyster spat appeared to set most readily on lower surfaces, whilst *Crepidula* exhibited a preference for upper surfaces.

The setting of the majority of species appeared to be governed by the same factors as those influencing oyster spatfall, as the numbers varied slightly in correlation with the suitability of the season for oysters. However, the steadily increasing rate of settlement of *Elminius modestus* on the test surfaces probably reduced the set of other sedentary forms.

Knight-Jones observed that *Membranipora lacroixi* may smother hundreds of oyster spat on collectors, but he did not find it on slates. This species was not recorded on slates in

Table 14: *Showing settlement of sedentary organisms on slates exposed for weekly intervals. Figures on left-upper surface, on right-lower surface of slate. Eggs of* Gobius minutus *occurred only on the undersides of slates and the figures indicate the numbers of times eggs were found on the slates*

Station and year	Ostrea edulis	Crepidula fornicata		*Post-larval molluscs*	Dendrodoa grossularia	*Bryozoa*	Tubularia larynx	*Other Coelenterates*	*Eggs of* Gobius minutus
		Post larvae	*Older individuals*						
1950									
Broadrakes	0/1	0/1	0/0	0/0	1/0	0/0	0/0	0/0	0
Shop Laying	15/24	7/17	0/0	1/0	0/0	0/0	0/0	0/1	0
Roach Mud	0/3	22/2	0/0	0/0	0/0	0/5	10/12	0/0	0
Bush Shore	3/5	39/4	0/0	1/1	0/3	0/4	0/0	0/0	0
Creeksea	14/22	56/6	0/0	0/0	1/3	0/1	0/1	0/0	0
Purleigh Shore	28/40	18/3	0/0	0/4	1/0	0/0	0/0	0/0	0
Fambridge	11/12	18/5	0/0	1/0	1/0	0/15	0/0	0/0	0
Totals	71/107	160/38	0/0	3/5	4/6	0/25	10/13	0/1	0
1951									
Broadrakes	0/0	0/0	0/1	0/0	0/1	0/0	0/0	0/2	0
Shop Laying	0/0	0/0	1/0	0/1	0/0	0/4	0/0	0/1	4
Roach Mud	0/0	0/0	0/0	0/0	0/0	0/0	0/0	8/7	0
Bush Shore	0/1	1/0	0/0	0/1	0/0	0/0	0/0	0/0	0
Creeksea	0/0	0/0	0/1	0/1	0/0	0/0	0/1	1/0	0
Purleigh Shore	0/0	0/0	0/0	0/2	0/0	0/1	0/0	0/1	3
Fambridge	0/0	0/0	0/0	0/0	1/0	0/7	0/1	0/0	4
Totals	0 1	1 0	1 2	0 5	1/1	0 12	0/2	9 11	11
1952									
Broadrakes	2/3	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0
Shop Laying	4/1	0/0	0/15	1/0	0/0	0/0	0/0	0/0	2
Roach Mud	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0
Bush Shore	5/3	2/0	3/3	3/0	0/0	0/0	0/0	0/0	0
Creeksea	6/4	0/3	0/0	0/0	0/0	0/0	0/0	0/0	1
Purleigh Shore	0/3	0/0	0/0	0/0	0/3	4/4	0/0	0/6	0
Fambridge	1/1	0/0	0/0	0/3	0/0	0/7	0/0	0/0	1
Totals	18/15	2/3	3/18	4/3	0/3	4/11	0/0	0/6	4
1953									
Broadrakes	0/1	0/0	0/0	0/0	0/2	0/0	0/0	0/0	0
Shop Laying	3/2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0
Roach Mud	0/2	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2
Bush Shore	2/0	3/0	0/0	0/0	0/0	0/0	0/0	0/0	0
Creeksea	0/2	1/0	1/0	0/0	0/0	0/0	0/0	0/0	0
Purleigh Shore	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0
Fambridge	0/1	0/0	0/0	0/1	0/0	0/0	0/0	0/0	0
Totals	5/8	4/0	1/0	0/1	0/2	0/0	0/0	0/0	2

this investigation but in 1950 and 1951 *Flustrella hispida* was observed on quarry tiles exposed at Purleigh Shore and Fambridge (Waugh, Hawes and Williams 1952). This species will also smother oyster spat on artificial collectors.

Tubularia larynx, which occurs on all floating surfaces in Essex rivers, occurred on the quarry tiles and slates though it rarely appeared on the collectors.

Ascidiella aspersa and *Ciona intestinalis*, although they never occurred on the slates, appeared in great numbers on the egg-box collectors, notably in the eddy at Black Point and in the upper Roach at Common Shore and Broadrakes. Well-grown spat were often found among the bases of these ascidians though barnacles rarely occurred in this situation.

Pomatoceros triqueter does not normally occur in Essex rivers but is frequently introduced on oysters from the river Fal and from Brittany. So too is the crow oyster *Anomia*. Whilst the latter has never been found setting in the Crouch and Roach, *Pomatoceros* is able to survive in limited numbers. A few newly-settled specimens were observed at Paglesham in 1948 but it was not again noted until 1951 when approximately 3 per collector of actively-growing worms were found at Roach Mouth. Since then they have been observed each year on collectors only. It seems possible that whereas a few adults might be able to survive on introduced oysters, the larvae are unable to settle and metamorphose on silt-covered oysters and shells on the bottom, but need clean surfaces raised clear of the bottom.

Curved tiles exposed in Althorne Creek in 1953 bore a dense population of sedentary forms such as *Ascidiella aspersa*, *Ciona intestinalis*, *Botryllus schlosseri*, *Sycon coronatum*, *Grantia compressa* and the scyphistoma stage of *Aurelia aurita*. Similar tiles exposed on Shop Laying bore practically nothing but *Elminius modestus* which was far more abundant than on the Althorne Creek tiles. The reduced quantity of silt in suspension in the creek probably accounts for the greater variety of sedentary animals. Turbidity is less too in the upper parts of the two rivers and here also there is a more varied fauna. This reduction in turbidity might well be an important factor influencing the set of oyster larvae which in such conditions have fewer *Elminius* with which to compete.

In the calmer, clearer waters of the creeks near West Mersea, at the mouth of the river Blackwater, the population of *Ascidiella*, *Ciona* and *Clavelina lepadiformis* is very dense but *Elminius* is not so abundant as in the muddy waters of the Crouch. It would appear, therefore, that turbidity has the two-fold effect of reducing the settlement of a great many sedentary organisms and of permitting the attachment of very large numbers of *Elminius*.

XIV. USE OF ARTIFICIAL COLLECTORS AND TYPES OF CULTCH

The intensity of spatfall during the five years has already been described (Section IX) and the use of collectors mentioned. The two types used were egg-box fillers, as used in Canada and Australia (Needler 1941; Kesteven 1941) and limed tiles (Dalido 1948). 'Bouquets' of small French tiles (Cole 1938), were set singly on stakes, so that they were raised above the bottom. Larger ridging tiles were stacked on the shore. They tended to trap silt and spat on them were vulnerable to attack by predators, particularly *Urosalpinx cinerea*.

In 1950 a random count of 19 ridging tiles gave a total of 180 spat or 9·5 spat per tile. Egg-box fillers yielded an average of 108 per collector, of four sections, over the same period. The total surface area of an egg-box collector is approximately 19,000 cm.^{2}, of which 5,000 cm.^{2} is upper horizontal surface which rapidly becomes covered with mud and unsuitable for any sedentary organisms. The effective setting area is therefore approximately 14,000 cm.^{2} The ridging tiles have a total surface area of 1,630 cm.^{2}, but because of their curvature, the whole of the upper surface does not normally become silted and approximately 1,400 cm.^{2} can be considered available for spat settlement. On this basis the catching capacity of the egg-box collectors and tiles is about the same, but the ease of handling of the collectors, plus the fact that they can be suspended from racks clear of the bottom, and so are relatively immune from attacks by drills, makes them more suitable as spat collectors.

Furthermore, losses on détroquage are less; the spat can be left undisturbed, attached to small pieces of the broken-up egg-box fillers.

In Essex, collectors of any type are subject to smothering by the barnacle *Elminius*, with consequent loss of spat. To combat this, collectors should be set out immediately preceding the major spatfall of oysters. In practice this was rarely practicable, as, in order to site them as far down the shore as possible, it was always necessary to put them out on the spring tides immediately preceding the expected spatfall. In consequence they were often heavily coated by barnacles before the oyster spatfall took place. Experiments made in 1950, on the use of a DDT dip for reducing barnacle settlement without affecting oyster spatfall, were unsuccessful (Waugh, Hawes and Williams 1952), but in 1953 and 1954 DDT sprayed on at the rate of 0·03 mg. per cm.^{2} proved satisfactory. An emulsion of 5% DDT solution (in a vapourising oil-benzene mixture), with water as a spreading agent, proved satisfactory.

In these experiments treated egg-boxes and controls were suspended at different places to ensure an adequate trial. Two different concentrations of DDT were used in 1953 and three in 1954. Oyster spat are sensitive to DDT so that it was necessary to use the minimum dose capable of reducing barnacle set without harming the oysters. The results show that reduction of fouling by barnacles allowed greater settlement of oysters (Table 15). Furthermore, growth of spat was better when they were not surrounded by barnacles.

Table 15*: The effect of varying dosages of DDT on the spatfall of* Ostrea *on collectors*

Station	*Treatment and mean number of spat per collector*			
	0·015 *mg./cm.*^{2}	0·030 *mg./cm.*^{2}	0·060 *mg./cm.*^{2}	*Control*
1953				
Shop Laying	217	387	—	142
Common Shore	123	140	—	75
1954				
Shop Laying	356	414	235	148
Broadrakes	152	182	122	96
Fambridge	46	93	95	55

To exploit local conditions, collectors were sited in the eddies at Black Point (1953 and 1954) and at the entrance to Bridgemarsh Creek (1954), Fig. 8, where Shelbourne (In press) had recorded concentrations of native oysters. The results, though promising, were not so good as had been hoped, because of the generally poor spatfall.

In 1952 bouquets were made of tiles which had been gravel-dashed after dipping in lime. Six bouquets of 8 tiles were set out on Shop Laying, together with six normal ones; at the end of September they yielded 505 and 332 spat respectively. The gravel-dashing increased the surface area of each tile and created more numerous 'micro-eddies' suitable for settlement.

It seems that collectors have limited commercial value in Essex as the densest spatfall during the five years yielded only approximately 300 spat per collector. Over the whole period the collectors averaged only approximately 120 spat in October. After wintering, the yield from each would have averaged less than 100 spat. The high aggregate cost of preparation, setting out, collection and détroquage, precludes their successful use unless a heavier spatfall can be assured.

The normal method of spat collection on the east coast is on cultch, usually cockle shell, spread over the grounds during the summer season, but small quantities are laid now compared with the hundreds of tons laid annually early in the century. Cockle shell is readily available, for there is an extensive bank of it on Foulness at the mouth of the river Crouch.

However, cockle shell tends to harbour the fungus of shell disease which now occurs in the rivers (Cole 1950), whilst mussel shell being more friable, is reputed not to do so (Korringa 1949). Accordingly, in 1950, a comparison was made of spatfall on cockle and mussel shell. On June 17 six strips, each 5 metres wide and 10 metres long, were marked out on Purleigh Shore so that they extended above and below low water of spring tides. Three were covered with cockle and three with mussel shell at the rate of 2·5 m.^{3} per strip. On August 21 random samples of approximately equal volumes of shell were collected; they were taken from the inshore and offshore ends of each strip and the numbers of shells and spat counted. Spatfall was between 4 and 5 times more intense on the mussel shell and was heaviest on the offshore ends of the strips (Table 16), just below low water mark.

Subsequent experiments have given similar results, but one, designed to compare settlement on untreated and DDT-sprayed mussel shell in 1954, failed as the spatfall was low; there were 9 spat on 200 sprayed shells and 8 on 200 untreated ones. This experiment will be repeated.

Table 16*: Showing spatfall on equal volumes* (450 *ml.*) *of cockle and mussel shell, laid on Purleigh Shore in* 1950*. The shells in the offshore strips were probably fewer because they were wet when collected and so displaced more water*

	Spatfall on mussel shell			*Totals*	*Spatfall on cockle shell*			*Totals*
Serial No. of Strip	1 *M.*	2 *M.*	3 *M.*		1 *C.*	2 *C.*	3 *C.*	
Inshore								
No. of shells	96	87	95	278	533	588	600	1,721
No. of spat	4	6	4	14	1	2	6	9
Offshore								
No. of shells	87	74	84	245	410	428	540	1,378
No. of spat	75	97	96	268	15	21	21	57

XV. LOSSES AMONG SETTLED SPAT

In 1952 clocks from Paglesham Reach were examined 14 days after peak settlement and bore an average of 4·6 spat per clock, whereas a month later the average was only 2·6—a mortality of nearly 50%. This does not agree with Knight-Jones' estimate of 90% mortality on tiles in the first month after settlement. Such heavy losses may have been due to predation by *Urosalpinx*. Drills commonly move on to tiles which can thus be used successfully as traps. Hancock (1954) estimated losses of older spat, more than 4 mm. in length, on Bush Shore and found that in 4 months the mortality was 75%, of which 57% was directly due to the activities of *Urosalpinx*. Losses of newly settled spat on this laying must have been very much greater.

Apart from predation, mortality may be caused by encrusting bryozoans and by silt. In addition spat settling in the direct run of the tide and subjected to bombardment by water-borne particles may suffer heavy losses (Shelbourne, in press). An advantage of collectors is that they offer sheltered, silt-free, surfaces for attachment and consequently losses, except by smothering bryozoans, are minimised. Nevertheless, losses on metamorphosis must be extremely heavy and may be influenced by the condition of the larvae which, if rapidly growing and of large size at settlement, probably have a better chance of survival.

XVI. DISCUSSION

Seasonal variation in the quantity of spat produced in the rivers Crouch and Roach, and indeed on the whole of the east coast, has been very great in the five years under discussion. Except in 1950, spatfall was insufficient to maintain the oyster population, so that present (1955) stocks are mainly derived from 1950 spat. In consequence there will be an acute shortage of mature native oysters at least until 1959.

The fluctuations in spat production can be related to known physical conditions of tide and weather but there are, in addition, several controllable factors which are of importance. Korringa (1947) has demonstrated that the total quantity of larvae produced is largely dependent on the size of the parent stock and in the present account it has been shown that, in the river Roach particularly, the production of larvae has fluctuated with the abundance of breeding oysters. Therefore, the maintenance of adequate stocks of these is of prime importance. This was demonstrated in 1950 when, though the proportion of larvae surviving to metamorphosis was less than in 1948, because of the much greater stocks, production of larvae was higher and spat more numerous. The existence of vast stocks of filter feeding organisms, particularly *Crepidula fornicata* (Mistakidis 1951; Cole and Hancock 1956; Walne 1956), suggests that food supply would suffice for an oyster population far in excess of the present one if such competing organisms were removed.

Restocking and attendant cultivation would provide more surfaces for spat settlement and would also consolidate the mud on the layings and so reduce turbidity. There is little doubt that the reduction in the quantity of water-borne silt, in addition to favouring growth and survival of oysters (Shelbourne, in press), would also result in a marked change in the benthic population of the two rivers. It has already been suggested (page 36) that turbid conditions favour the barnacle *Elminius modestus*, but any reduction in its numbers due to cleaner water might well lead to an increase in the numbers of ascidians, etc. Well-planned cultivation, particularly in the early summer, besides providing more clean surfaces for spat settlement, would reduce the benthic predators and consequently the losses of oyster larvae. Certainly results obtained in 1953 suggest that the spatfall would be heaviest on the cleanest and most densely stocked grounds.

Larvae are also lost by dispersion and this could be limited by well-planned siting of mature oyster stocks. Except in 1950, spatfall has occurred in the lower reaches of the river Crouch but Brandy Hole and the upper reaches have always had the reputation of being extremely good spatting grounds. The reason for this probably rests on the fact that the bottom there is gravelly and hard, is periodically scoured clean of sedentary competitors by fresh water in winter, is almost completely free of *Urosalpinx* and is situated in an eddy area. It is, therefore, very suitable for spat settlement in comparison with the extensive uncultivated muddy areas further downstream.

The laying of mature oysters in the upper reaches, for their final season before marketing, would tend to shift the focus of larval production further upstream and so minimise the loss of larvae by dispersion if, as appears probable, there is at times a substantial loss of river water out to sea. Furthermore, spat would tend to settle in the middle and upper reaches of the Crouch where conditions are most suitable. Such a system would mean a radical change in the present method of cultivation because, though the practice has been to dredge all young oysters from the upper reaches at the end of each season and relay them in deeper water downstream, where they are less likely to be affected by low salinity and extreme cold, no large scale attempts have been made to lay stocks of breeding oysters in the upper Crouch. The suitability of such grounds for fattening oysters in their last season would, of course, have to be tested. In the river Roach conditions are different in that the lower reaches are unsuitable for oyster production, due mainly to scour or mud.

Water temperatures do exert an influence on the growth rate and survival of the larvae, but are never likely to be so low as completely to prevent spatfall. In the exceptionally cold summer of 1954 a proportion of the larvae reached the eyed stage though it is certain that if temperatures had been higher more would have survived to metamorphosis. A more important factor seems to be the influence of the condition of the parent stocks on the size

and viability of the larvae, which can in turn be related to the conditions to which the oysters were subjected during the time they were maturing sexually. This poor viability, noted particularly in 1951, has also been recorded by Cole (1936), who concluded that oysters kept too long under tank conditions produced non-viable larvae. Therefore, oysters relaid specifically for breeding purposes need to be carefully selected and in the best possible condition.

The food supply for the adult oysters in the rivers has not been studied, but probably varies in much the same way as the population of 2–10 μ flagellates, because in summers of good larval growth there has been correspondingly good oyster growth. The population of these flagellates is not so stable as Knight-Jones (1952) suggested and there is evidence that grazing by oyster larvae and other filter feeders does result in an appreciable drop in their numbers. The main conditions necessary for good larval growth in natural waters would appear to be adequate supplies of food and suitable water temperatures (Imai *et al.* 1951). Any method which ensures that there is an abundance of rapidly multiplying flagellates at the time of peak oyster larval production will have a marked effect on the degree of survival of the larvae and to a more limited extent on their rate of growth for, whilst it appears that scarcity of food organisms such as occurred in 1951 has the effect of retarding growth, there is no evidence that rapid growth will occur if there is an abundance of food unless temperatures, too, are suitable. Experiments to date indicate that the use of artificial fertilisers might well serve to increase the flagellate population and that the river Crouch is suitable for such experiments because introduced nutrients are retained for a considerable period. Phosphate, however, is not apparently the limiting substance as it is naturally abundant in the two rivers. There must be more than adequate reserves locked up in the mud, which are released by wave action and also by dredging. The controlled release of flagellate-rich water from saltings and ditches behind the sea wall would also serve the purpose of augmenting food supply for the larvae. In neither case is it likely that the population would be so dense as materially to alter the pH, which does not normally exceed 8·2 and is well below a harmful level (Cole 1936; 1939).

Spatfall forecasts, and advice to oystermen of the best times at which to lay cultch, will be continued, so ensuring that larvae about to metamorphose have the maximum opportunity for survival. The advantages of such forecasts are obvious but the tremendous increase in the numbers of *Elminius modestus* has made it particularly important that clean surfaces should be available at the time of the oyster spatfall.

SUMMARY

Continued observations of the production and growth of the oyster larvae have led to a clearer understanding of conditions necessary for a successful spatfall. Preliminary study of the hydrography of the rivers Crouch and Roach indicates that the water movement is not always piston-like and that wind can exert an appreciable influence on water movement.

Nanoplankton flagellates between 1 and 10μ, the size suitable as food for oyster larvae, vary considerably in number. It appears that they multiply most rapidly during periods of neap tides when losses due to water transport are least and light penetration, because of reduced turbidity, is greatest. The possibilities of augmenting the flagellate population are discussed.

Examination of 100 litre plankton samples, pumped regularly from widely separated stations in the two rivers, yielded information on the abundance and growth of the oyster larvae. Larvae were usually liberated after the water temperature had exceeded 18°C. and there is evidence that temperature rather than the state of the tide, i.e., spring or neap, is the main factor governing spawning. The act of liberation, however, almost invariably occurred at high tide and was apparently completed in a very short time.

Duration of the planktonic stage varied considerably and was related mainly to water temperature though there is evidence that shortage of flagellate food results in prolongation

of the larval stage. Certainly rapid development and good survival are associated with an abundance of flagellates. Heavy larval mortalities may also be due to poor viability and it is suggested that unfavourable conditions in the early spring result in parent oysters producing larvae with poor food reserves and reduced viability. When the growth of the adult oysters is poor, the larvae, at liberation, are smaller in size than when growth is good. Study of the distribution of the larvae explains how, under certain conditions of wind and tide, physical loss of the larvae, out to sea, can occur.

Changes in the abundance of breeding stocks have been reflected by changes in the numbers of larvae produced. For example, a drop in larval numbers in 1953 was attributable to the big mortality of adult oysters in the spring of that year.

Methods of recording spatfall are not completely satisfactory. Slates exposed for weekly intervals give misleading information partly because the exceedingly dense settlement of *Elminius modestus* seriously interferes with the settlement of oyster spat and other sedentary organisms. In assessing spatfall, consideration must be given to the cleanliness of the test surfaces, the distribution of adjacent settling surfaces, the abundance of oysters in their immediate vicinity and the abundance and distribution of oyster larvae, about to settle, in the water. Seasonal variation in spatfall during the years 1950 to 1954 was substantial, it was moderate in 1950, a complete failure in 1951 and light in the other three years.

Heavy winter losses in the upper Crouch are associated with low salinity rather than extreme cold. Heavy rainfall in winter causes a substantial run off from the land. This can result in the salinity of the upper Crouch dropping to well below $20^{0}/_{00}$.

The population of *Elminius modestus* in Essex has now reached a very high level and this barnacle seriously interferes with the set of oyster spat. Experiments with artificial collectors show that oyster spatfall on a given surface can be doubled if the surface is treated with DDT in such a way as to prevent barnacle settlement. Oyster spat surrounded by dense barnacle populations appear to grow only slowly. It is, therefore, essential that cultch should be laid as near as possible to the time of oyster spatfall. This makes accurate forecasting of the time of spatfall particularly important.

Limed tiles and egg-box fillers coated with cement are efficient spat collectors but they are unlikely to have any economic application unless heavier and more regular spatfalls can be assured. Cockle shell cultch, as used at present, is satisfactory but, volume for volume, mussel shell is far more efficient for spat collection. Apart from spat collection it is likely that the considerable quantities of shell laid in earlier years helped to bind the mud and so reduce the quantities of water-borne silt which, it is suggested, seriously interfere with the growth of both adult and larval oysters.

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